Leadership and Group Decision-Making in Banded Mongooses (*Mungos mungo*)

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CONTENTS

SUMMARY

Animals living in stable groups need to make communal decisions regarding which activities to perform, when to perform them and in which direction to move. In social species it is important that these decisions are made together with other group members since the group will split apart unless a consensus is reached. Loosing contact with the group may have severe fitness consequences for the individual. To get a clearer understanding of decision-making processes one should focus on who is involved in the decision-making, what mechanisms underlie group decisions and the potential resulting fitness consequences. In my thesis, I investigated leadership and group decisions in a wild but habituated population of banded mongooses (*Mungos mungo*) in their natural habitat. These small carnivores breed cooperatively, with an egalitarian social structure. In particular, I focused on factors influencing leadership in group departure, group decisions in a potentially dangerous situation and an acoustic mechanism to recruit other group members to the location of the caller(s).

I show that leadership in group departure is highly variable and that neither sex nor age had influence on the likelihood to initiate group departure. However, during periods of synchronized breeding pregnant females tended and lactating females initiated group departure more often than expected. These findings suggest that the individual's reproductive state has a higher influence on leadership in group departure than the individual's identity. Further investigation on the influence of the individual's state on leadership showed that the initiators' body weights in relation to the weight of the previous day were not lower than during a control period, suggesting that bad foraging success did not affect leadership. However, results from feeding/deprivation of food experiments showed that low energetic reserves tended to influence the likelihood to initiate group departure. These findings suggest that nutritional constraints can have an influence on leadership but often other factors also play important roles. To study group decisions in a potentially dangerous situation, I simulated an intruding group of banded mongooses with playback experiments of screeching calls. When banded mongooses spot rival groups of mongooses, individuals emit these calls, which cause the group to gather at the caller's location. I showed that the location of the simulated inter-group encounter and the group size of the resident group influenced its decisions to approach the loudspeaker or to retreat. Most test groups responded context-specifically and approached in the core zone of their territory, but retreated in the overlap zone. However, the largest group always approached and the smallest group always retreated, suggesting that experience of previous contests plays an important role in the decision-making process. Acoustic analyses of recruitment calls produced when banded mongooses encounter predator secondary cues, snakes or rival mongooses, revealed that the call structure varies according to risk and not stimuli type. Receivers extracted meaningful information from calls. A higher proportion of subjects responded, and they also did so faster, to playbacks of calls recorded in situation of higher risk. These calls allow group members to gather quickly at the location of the callers, which enables group members to make appropriate decisions in response to the stimuli.

Together, these results show that in banded mongooses, which live in an egalitarian society, many different individuals can be involved in decision-making processes. While the individual's state appears to be a key determinant of leadership, other social and ecological factors also influence group decision-making. Furthermore, different vocalisations are used in several contexts to coordinate group activities which allow communal decision-making. Given the different individuals who can be involved in group decision making processes, banded mongooses provide a strong contrast to results gained from species that live in more despotic societies showing consistent involvement of certain individuals in group decisions.

ZUSAMMENFASSUNG

Tiere, die in Gruppen leben, müssen häufig gemeinsam Entscheide treffen. Beispielsweise entscheiden sie, welche Aktivitäten sie ausführen, wann sie eine Aktivitätsänderung machen und wohin sie gemeinsam gehen. Für soziale Arten, die in stabilen Sozialverbänden leben, ist es wichtig, Entscheide gemeinsam mittels Konsens zu treffen. Falls keine Übereinstimmung erreicht werden kann, gehen einzelne Gruppenmitglieder häufig getrennte Wege. Eine solche Aufteilung in Untergruppen kann aber mit hohen Kosten verbunden sein. Untersuchungen zeigen, dass soziale Tiere, die den Kontakt zu den anderen Gruppenmitgliedern verlieren, oft kleinere Überlebenschancen haben und weniger Nachkommen produzieren. Um die Prozesse der Entscheidungsfindung bei sozialen Tieren besser zu verstehen, gilt es, die folgenden Fragen zu beantworten: 'Welche Individuen sind bei der Entscheidungsfindung involviert?', 'Mit welchen Mechanismen werden Entscheide gefällt?' und 'Welche Konsequenzen in Bezug auf den Reproduktionserfolg bringen die Entscheide mit sich?'. In meiner Dissertation untersuchte ich Gruppenentscheide bei wilden, aber an den Mensch gewöhnten Zebramangusten (*Mungos mungo)* in ihrem natürlichen Lebensraum. Zebramangusten sind kleine, soziale Raubtiere, bei welchen neben den Eltern auch die anderen Gruppenmitglieder bei der Aufzucht der Jungtiere mithelfen. Ich fokussierte mich einerseits auf Faktoren, welche die Koordination des gemeinsamen Abmarschs vom Schlafbau beeinflussen, andererseits analysierte ich Gruppenentscheide, die bei Gefahr getroffen werden müssen. Ausserdem untersuchte ich spezifische Rufe, die dazu führen, dass sich alle Gruppenmitglieder am Ort der rufenden Tiere versammeln.

Meine Resultate zeigen, dass viele verschiedene Tiere den gemeinsamen Aufbruch der Gruppe einleiten können. Weder Alter noch Geschlecht der involvierten Tiere scheinen einen massgeblichen Einfluss auf die Entscheidungsfindung zu haben. Allerdings zeigte sich, dass während der Zeit, in der die Weibchen Junge säugen, die säugenden Weibchen häufiger in die Entscheidungsfindung involviert sind, als erwartet. Es scheint also, dass bei Zebramangusten der reproduktive Zustand des Individuums einen grösseren Einfluss auf das Mitwirken in der Gruppenentscheidung hat als Alter und Geschlecht. Des Weiteren untersuchte ich mit Gewichtsanalysen and Feldexperimenten, ob Individuen, die am Vortag nur wenig Nahrung aufnehmen konnten, am folgenden Tag eher aktiv den Gruppenabmarsch einleiteten. Es zeigte sich, dass einerseits Tiere, die am Vortag wenig fressen konnten, häufig den Gruppenabmarsch einleiten, andererseits aber viele andere Faktoren einen wichtigen Einfluss auf die Koordination des Gruppenabmarschs haben können. Gegenüber Eindringlingen verteidigen Zebramangusten aktiv ihr Revier. Wenn eine Gruppe Zebramangusten auf eine andere Gruppe trifft, produzieren die Individuen oft spezifische Rufe. Mittels Playback dieser Rufe simulierte ich eine feindliche Gruppe, die das Revier der dort ansässigen Gruppe betrat. Ich analysierte, ob sich die Revier-Gruppe den Lautsprechern, welche die Rufe abspielten, annäherte oder ob die Revier-Gruppe wegrannte. Es zeigte sich, dass die Revier-Gruppe in der Mitte ihres Reviers auf die imaginären Eindringlinge zu rannte, während sie am Rand ihres Reviers wegrannte. Neben dem Ort hatte auch die Gruppengrösse der Revier-Gruppe einen Einfluss auf den Gruppenentscheid. Grössere Gruppen rannten eher auf die Lautsprecher zu als kleinere. Es scheint also, dass eine Kombination der Faktoren Ort im Revier, Gruppengrösse der Revier-Gruppe und Erfahrung aus vorherigen Zusammenstössen mit anderen Gruppen für die Gruppenentscheide in dieser simulierten Gefahrensituation verantwortlich sind. Ähnlich zu den Rufen, welche Zebramangusten beim Entdecken von anderen Gruppen ausstossen, produzieren sie auch Rufe, wenn sie Raubtierkot oder Fressfeinde wie Schlangen entdecken. Ich untersuchte mit akustischen Analysen und Playback-Experimenten den Informationsgehalt dieser Rufe. Die Resultate zeigen, dass sich die akustische Struktur der Rufe anhand der Dringlichkeit der Situation verändert. Die Rufe zeigen aber nicht eine stimulus-spezifische Struktur. Mit Playback-Experimenten konnte ich zeigen, dass die Testtiere sich spezifisch zur

Struktur der abgespielten Rufe schneller oder langsamer dem Lautsprecher annäherten. Auch zeigte sich, dass bei Rufen die unter erhöhter Dringlichkeit aufgenommen wurden, ein höherer Anteil der Testiere beim Lautsprecher ankam. Diese Rufe ermöglichen es den Gruppenmitliedern sich bei Gefahr schnell am Orte des Geschehens zu versammeln und anschliessend gemeinsam Entscheide zu treffen.

Die Resultate meiner Dissertation zeigen einerseits, dass bei Zebramangusten, welche in einem egalitären Sozialsystem leben, bei dem viele Weibchen gleichzeitig Junge werfen, verschiedene Individuen bei der Entscheidungsfindung eine tragende Rolle übernehmen können. Für die aktive Teilnahme an Gruppenentscheiden kann andererseits der momentane Zustand eines Individuums wichtiger sein als sein Alter und Geschlecht. Ausserdem können diverse soziale Faktoren (bspw. Gruppengrösse) und Umweltfaktoren (bspw. Ort des Geschehens) Gruppenentscheide stark beeinflussen. Schliesslich spielen Vokalisationen eine wichtige Rolle bei der Koordination der Gruppenaktivitäten und ermöglichen so eine gemeinsame Entscheidungsfindung. Da viele verschiedene Individuen in Prozesse der Entscheidungsfindung involviert sein können, stehen Zebramangusten im Kontrast zu Arten mit klarer Dominanzhierarchie, bei welchen häufig nur einige wenige Individuen bei Gruppenentscheiden involviert sein können.

GENERAL INTRODUCTION

General Introduction

Group decision-making in animal societies

In human and animal societies, group decisions are essential to coordinate activities between individuals (Bonabeau et al. 1997; Seeley & Buhrman 1999; Franks et al. 2002; Conradt & Roper 2003; List 2004; Conradt & List 2009). Group decisions are defined as decisions made by the individuals within a group and are divided into 'consensus' or 'combined' decisions (Conradt & Roper 2005). In social species that live in stable groups, the maintenance of group cohesion is crucial if individuals are to benefit from the advantages of group living (Alexander 1974; Krause & Ruxton 2002), such as the increased likelihood of finding food or detecting predators (Pulliam & Caraco 1984, Giraldeau & Caraco 2000). To synchronize activities, group members regularly need to make decisions through a consensus process to ensure that groups do not fragment (Conradt & Roper 2003; Conradt & Roper 2005). To make such consensus decisions, individuals choose between two or more mutually exclusive activities, such as foraging and resting, with the specific aim of reaching a consensus (Conradt & Roper 2005). Individuals, however, may differ in their foraging efficiencies, energetic needs and/or knowledge about the environment. Therefore, conflicts of interest about the timing of mutually exclusive activities might arise, resulting in 'consensus costs' for certain group members (Conradt & Roper 2003; Conradt & Roper 2005). Such consensus costs develop when group members need to compromise their optimal activity budgets in order to make consensus decisions. Thus, the costs of making consensus decisions might be a major factor in shaping the organization of social animals (Prins 1996; Conradt 1998; Ruckstuhl & Neuhaus 2002).

Combined decisions commonly occur in species living in transient aggregations of animals, such as large flocks of migrating birds or fish swarms (Conradt & List 2009), or in fission-fusion societies where individuals regularly form subgroups without permanently leaving the society (Aureli et al. 2008). In this type of group decision, group members choose individually between two or more actions without aiming for a consensus and as a result, group splits commonly occur (Conradt & Roper 2005). Such combined decisions can be beneficial in situations where a consensus cannot be reached because of time constraints or

strong conflicts between group members (Franks et al. 2003; Kerth et al. 2006; King et al. 2008; Conradt et al. 2009).

Empirical evidence suggests that consensus and combined decisions result from the same decision-making processes. The outcome of the decision might often depend on the situation, and in particular whether grouping benefits are bigger than the consensus costs (Biro et al. 2006; Kerth et al. 2006; King et al. 2008; Kerth in press). Consensus decisions occur frequently in spatially cohesive groups (Conradt 1998) where they typically occur in the context of travel destinations (Stolba 1979), movement directions (Couzin et al. 2005) and activity timing (Stewart & Harcourt 1994). To get a deeper understanding of decision-making processes it is essential to focus on the following questions: i) Who makes the decisions? ii) What are the underlying mechanisms? iii) What are the fuctions and fitness consequences of group decisions? (Conradt & Roper 2005).

Who makes the decisions?

The number of group members involved in a decision-making process varies greatly. Decisions may be made by one animal (despotic or unshared decision; Norton 1986; Byrne 2000; Milton 2000), a particular subset of group members (partially shared decision; Seeley & Buhrman 1999; Mallon et al. 2001), or by all group members (democratic or equally shared decision; Norton 1986; Prins 1996). Shared decisions appear to decrease group consensus costs and may provide additional benefits via information pooling (List 2004). Major factors influencing group decisions are the distribution of information among group members (Reebs 2000; Swaney et al. 2001; Franks et al. 2002; Seeley 2003; List 2004; Simons 2004), conflict of interest between individuals (Conradt and Roper 2003; Conradt and Roper 2005) and time constraints (Conradt and Roper 2005). Information may be available to all individuals (public), or it may be restricted to a single individual or a subgroup (private) (Conradt & Roper 2005). When the degree of information varies among group members, theoretical models still predict democratic decisions in most instances (List 2004; Simons 2004). Despotic decisions are only expected when the difference in information is large and group size is small. For example in African elephants (McComb et al. 2001) and some primates (Byrne 2000), it is the older individuals that emerge as 'leaders' or 'initiators' of group decisions. In situations where conflicts of interest between group members appear to affect group decisions, conflicts may be caused by differences in age, sex, dominance status and physiology, or when individuals differ in relatedness (Conradt & Roper 2005). Group

members often resolve conflicts by making democratic decisions (Conradt & Roper 2003). However, during such conflicts of interest, it may be advantageous for an individual to use gathered information to bias the decision-making process for its selfish interest (Franks et al. 2003). Although group members may attempt to influence the outcome of a decision, time constraints may ultimately override all other factors. When fast decisions are needed, all group members are likely to benefit from following the decision of the best informed individual. For example, house-hunting ant colonies adjust their 'speed-accuracy' trade-off in harsh environmental conditions, with nest sites being chosen more quickly in windy weather than in calm weather. To choose new nest sites faster, ants rely more heavily on individual decision-making than on collective decision-making (Franks et al. 2003). Therefore, situations requiring fast responses should favour despotic decisions (Franks et al. 2003; Passino & Seeley 2006).

In relatively small, spatially cohesive groups, where members can communicate globally (i.e. with all other group members; Conradt & Roper 2005), it has been shown that decisions regarding when to leave a location and where to forage are often led by a single individual (Conradt & Roper 2005). Such leadership in group movement can be consistent, with the same group member almost always initiating activity changes (Kummer 1968; Dunbar 1983; Dumont et al. 2005). Alternatively, leadership in group activities can be variable, with different group members leading group actions on different occasions (Lamprecht 1992; Leca et al. 2003; Radford 2004). Consistent leadership in group movement might be influenced by knowledge about where to find certain important resources (Reebs 2000; Swaney et al. 2001; Franks et al. 2002; Seeley 2003), the species' social organization (e.g. influence of social dominance: Schaller 1963; Erhart and Overdorff 1999; Jacobs et al. 2008; Sueur and Petit 2008) or personality characteristics (Ward et al. 2004; Leblond & Reebs 2006; Harcourt et al. 2009; Kruvers et al. 2009). Whilst the causes of consistent leadership in group movement are relatively well understood, little is known about the causes of variable leadership. Game-theoretical models predict that in a pair of animals the individual with lower energetic reserves should emerge as the leader. Leaders determine when the pair should forage as they initially gain more from this activity than the other member of the pair (Rands et al. 2003; Cant & Shen 2006). Individuals with the strongest need for change at a given time often emerge as initiators of group movement and therefore, nutritional constraints might underlie variable leadership roles.

What are the mechanisms underlying group decisions?

Group decisions made by more than one individual require mechanisms to facilitate the coordination of preferences of the individuals involved. 'Voting' has been described as the main mechanism of shared group decision-making, whereby individuals communicate their preference with regards to the decision outcome (Boinski & Campbell 1995). Voting behaviour has been described to be expressed by specific vocalizations (Poole et al. 1988; Stewart & Harcourt 1994; Boinski & Campbell 1995), ritualized signals (Black 1988), body orientation (Norton 1986; Prins 1996), and initiation of movements (Byrne 2000; Milton 2000). It has been suggested that group members can estimate the number of votes and therefore reach a consensus decision via a quorum (minimum number of animals that need to take or favour a particular action for the whole group to adopt this action; Pratt et al. 2002; Seeley & Visscher 2004). Apart from studies in insects, little is known about this process of decision-making via quorum sensing. In large groups, often self-organizing rules (an individual follows the local behavioural rules in response to its neighbours which results in organised behaviour without the need for global control) could lead to equally shared consensus decisions (List 2004; Couzin et al. 2005).

Aims of research

To clarify the importance of different factors contributing to consensus decision-making it is essential to study animals where life-history data on age, sex and reproductive state are available. In addition, to investigate mechanisms involved in group decisions, it is important to study group decision-making under natural conditions. By focusing on habituated individuals that live in relatively small, stable groups it might be possible to elucidate the subtle mechanisms in decision-making. In my thesis, I focus on leadership and decision-making in banded mongooses, a cooperative breeder with an unusual reproductive behaviour. In contrast to closely related species that have a dominant breeding pair (e.g. meerkat and dwarf mongoose), in banded mongooses multiple females breed in synchrony (Cant 2000). Banded mongooses offer a unique opportunity to investigate the influence of an 'egalitarian' social organization on decision-making, and to compare and contrast these findings with results from closely related species with more despotic social systems. Comparing related species with different social organization will help to identify and clarify the key determinants

that influence individual contributions to group decisions such as age, reproductive state and dominance.

Study species

Banded mongooses are classified within the order Carnivora and the family Herpestidae (Kingdon 1997). There are 24 species of mongoose in Africa, the majority of which are solitary and nocturnal (Kingdon 1997). Together with the meerkat, dwarf mongoose, Somali dwarf mongoose, Gambian mongoose and four species of cusimanse, the banded mongoose is a social and diurnal species. Banded mongooses are widely distributed in sub-Saharan Africa and have a broad habitat tolerance ranging from woodland to open savannah (Skinner & Smithers 1990). Groups den in termitaria, hollow trees and crevices and change overnight dens frequently. Cant (1998) found that social groups changed dens every two nights on average. After emerging from the den the whole group departs 'en masse' with individuals ordinarily moving in a file, either single or up to three animals abreast. When foraging, group members are often more spread out but group cohesion is maintained by contact calls (Rood 1975). During foraging, banded mongooses face many communal decisions about when to leave a foraging patch, where to go next and what to do when a predator is encountered. Consensus decisions appear to be commonly made as group splits only rarely occur.

Banded mongooses live in stable, mixed-sex groups consisting of around 25 individuals (range: 6 to 50 individuals, although groups can temporarily be as large as 70, Cant 2000; Cant 2003). Groups breed up to four times per year and little or no reproductive skew occurs among females (Cant 2000). Among cooperative breeding species, reproductive skew can be seen as a continuum, from despotic societies of singular breeders, to more egalitarian societies of plural breeders (Keller and Reeve 1994). In banded mongooses, multiple females come into oestrus in synchrony, become pregnant and usually give birth on the same day (Cant 2000). Group members assist in rearing pups by 'babysitting' them at the den for the first four weeks of life (Cant 2003) and by provisioning pups with food items until they are able to forage independently (Gilchrist 2004; Hodge 2005). Pup care is strongly male biased, with males contributing more to babysitting and pup feeding (Hodge 2007). In contrast to many other mammal species, both sexes may remain in their natal group beyond the age of sexual maturity, and some individuals of both sexes reproduce and die within their natal pack (Cant

1998). In addition to the rather equal distribution of female reproduction, there is no obvious social dominance hierarchy (although De Luca & Ginsberg (2001) found a linear dominance hierarchy among group members of both sexes, no obvious linearity was found in further studies). Thus, banded mongooses provide an excellent opportunity to study group decision-making in a more egalitarian society (De Luca & Ginsberg 2001) with low reproductive skew amongst females (Cant 2000), no philopatric sex (Cant 1998) and no obvious linear dominance hierarchy.

Banded mongooses feed on invertebrate and small vertebrate prey (Rood 1975). To find their food, they have to roam widely because their prey is not bound to just a few locations in their relatively small home ranges (average home range size: 90.5 ha; cf Gilchrist and Otali 2002). While banded mongooses compete within groups for access to food and mates, they also compete between social groups for food, space and access to mates (Cant et al. 2002). Home ranges of neighbouring groups often overlap, and social groups engage in cooperative territorial defence. Banded mongooses mark their home range with faeces, urine and secretions of the anal glands which are inspected intensively when encountered by neighbours (Rood 1975; Müller and Manser 2007). Competition between social groups is intense, with frequent inter-group encounters and often including physical contact, severe aggression and on occasion fatal injuries (Rood 1975; Cant et al. 2002; Gilchrist and Otali 2002; Müller and Manser 2007). Due to their relatively small body size and their diurnal foraging habits, banded mongooses are susceptible to predation by aerial and terrestrial predators. Hence, predator avoidance is an integral part of a mongoose's life (Müller 2007). The adaptive significance of group life to banded mongooses, in protection from predators and in caring for offspring (Rood 1975), makes them an ideal study species to investigate consensus decision-making and leadership roles.

Study site and population

The data presented in this thesis were collected from July 2006 to December 2007 on a wild but habituated population of banded mongooses living on and around Mweya Peninsula, Queen Elizabeth National Park, Uganda (0°12'S; 29°54'E). The study population consisted of six habituated social groups allowing close-range observations and field experiments. Additionally, I collected data on the spatial distribution of two semi-habituated groups and

one wild group. Group sizes ranged from 7 to 44 individuals and the habituated population consisted of approximately 150 adult individuals and their offspring. The population of banded mongooses on and around Mweya Peninsula was studied in the 1970s by Jon Rood and again from 1994 onwards by a succession of PhD students (Cant 1998; De Luca 1998; Gilchrist 2001; Hodge 2003; Bell 2006; Müller 2007). I had access to life-history data from the last 12 years collected by previous PhD students. I used GPS data collected by all field researchers present between July 2006 and December 2007 (PhD students: Neil Jordan, Bonnie Metherell and myself; research assistants: Francis Mwanguhya and Solomon Kyabulima). All other data were collected by my research assistant Solomon Kyabulima and myself.

With an annual precipitation of 800-1000 mm (Rood 1975; Gilchrist 2001) the habitat of the study site consists of mainly short grassland dotted with numerous dense thickets (mainly containing *Capparis tomentosa*, *Azima tetracantha)* interspersed with Euphorbia trees (*Euphorbia candelabrum*) (Lock 1981). The temperature fluctuates little throughout the year, with a mean daily temperature of 23-26 °C (Cant 1998). Although rain may fall in any month, the main rainy seasons are March to May and September to November. Generally, the driest periods last from January to February and from June to July (Rood 1975; Gilchrist 2001). Banded mongooses share the habitat with large herbivores (African elephant, hippopotamus, African buffalo, waterbuck, bushbuck, Uganda kob, giant forest hog, warthog), primates (vervet monkey and olive baboon, the latter is very rare at the study site) and a plethora of birds species. Potential mammalian predators of adult or juvenile banded mongooses include other solitary and nocturnal herpestids (Egyptian mongoose, white-tailed mongoose), the rusty-spotted genet and large carnivores. Lions were common at the study site. In 2007, we frequently encountered up to nine lions (2 males, 2 females and 5 cubs). In contrast, leopards were spotted infrequently and seemed to be less common than in the recent past (Corsin Müller, personal communication). Spotted hyaenas appeared to be much less common than a few years ago when up to 16 individuals were seen at the same den in the study site (Francis Mwanguhya, personal communication). Of the dazzling array of birds of prey encountered at Mweya, banded mongooses have been observed to respond strongly to the following species: African marsh harrier, martial eagle and yellow-billed kite. Additionally, pups are frequently predated by marabou storks. Predatory reptiles include African rock python and monitor lizard.

Banded mongooses gathering just after having emerged from the den.

Banded mongooses on the way to Mweya village.

Typical habitat at the Mweya peninsula consists of short grassland interspersed with thickets. Banded mongooses share this habitat with many other animal species (e.g. left: Uganda kob; right: African buffalo)

Predators that occur at Mweya and potentially prey on banded mongooses. Left: martial eagle (here an immature individual), middle: leopard, right: lioness.

Outline of thesis

In my thesis, I investigate leadership and group decision-making in banded mongooses. Based on the main questions stated by Conradt and Roper (2005) I examine who is involved in decision-making processes, what factors affect the decision-making and what kind of decisions are made. Furthermore, I also focus on the field of communication by analyzing an acoustic mechanism leading to the recruitment of group members, which then allows for communal decision-making. The **first chapter** deals with the initiation of group departure which is, after emerging from the den, the first important decision in coordinating the group activity in banded mongooses. I examine who is initiating group departure and in particular whether specific group members or specific subgroups of individuals are more likely to initiate group departure. To do so, I analyse whether certain factors like sex, age and reproductive state influence leadership roles in banded mongooses. In **chapter 2**, I turn the attention to whether low energetic reserves may influence an individual's likelihood to initiate group departure. Based on game-theoretical modelling by Rands and colleagues (2003) stating that in a pair of foraging animals the individual with lower energetic reserves should become the pacemaker in leading the pair during foraging, I analyse whether the initiators weight in relation to the previous day is lower compared to a control period of two days. Moreover, I test with deprivation of food/feeding experiments whether food-deprived individuals are more likely to initiate group departure on the next morning. I then compare the predictions from theoretical modelling on foraging pairs with my findings in groups of more than two individuals. The **third chapter** of my thesis deals with group decisions in a potentially dangerous situation. With playback of rival groups' screeching calls I simulate an impending inter-group encounter. Such contests between social groups are common in banded mongooses and can have fatal consequences. I focus on the immediate and the final decision of the resident group and analyse what factors might influence the resident group’s decisions. In **chapter 4**, I explore an acoustic mechanism that recruits the other group members to the location of the caller(s). Banded mongooses emit such calls when encountering secondary predator cues or ambush predators such as snakes and rival conspecifics. After recruitment, group members gather together and inspect or mob the eliciting stimuli. The involved information gathered by the recruited group members allows for appropriate group decisions in response to the stimuli. With acoustic analyses I investigate whether calls show structural differences according to the different stimuli. With playbacks I test whether the informational content differs for the receivers between calls emitted in different contexts. In the **final**

chapter, I discuss my findings and their relevance for the growing literature on group decision-making and leadership in animal societies. This study provides data on leadership and group decisions in a cooperatively breeding mammal species with low reproductive skew and an egalitarian social structure. The availability of life-history data and the good habituation level of six study groups allow me not only to analyse the influence of factors like age, sex, reproductive state and weight gain in wild animals but also to experimentally test predictions from theoretical models. My research provides insight into group decisions and factors affecting them in a free-ranging mammal species. My study provides a significant contribution to our knowledge about group decision-making in animal societies living under natural condition. As such, this study makes it possible to compare and contrast the group decision processes in wild animals, with findings of theoretical models and studies conducted on captive or semi-free ranging animals. Chapters 2 to 4 have a strong focus on experimental research and are therefore an important complement to experiments on group decisions conducted in the laboratory.

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Appendix

Scientific names of species mentioned in this chapter

MAMMALIA

Bovids (Bovidae)

African buffalo	*Syncerus caffer*
Bushbuck	*Tragelaphus scriptus*
Uganda Kob	*Kobus kob thomasi*
Waterbuck	*Kobus ellipsiprymnus*

Cats (Felidae)

Leopard	*Panthera pardus*
Lion	*Panthera leo*

Cheek-pouch monkeys (Cercopithecidae)

Olive baboon	*Papio anubis*
Vervet monkey	*Cercopithecus aethiops*

Elephants (Elephantidae)

African elephant	*Loxodonta africana*

Genets and Civets (Viverridae)

Rusty-spotted genet	*Genetta maculata*

Hippopotamuses (Hippopotamidae)

Hippopotamus	*Hippopotamus amphibius*

Hyaenids (Hyaenidae)

Spotted hyaena	*Crocuta crocuta*

Mongooses (Herpestidae)

Alexander's cusimanse	*Crossarchus alexandri*
Ansorge's cusimanse	*Crossarchus ansorgei*

Banded mongoose	*Mungos mungo*
Cusimanse	*Crossarchus obscurus*
Dwarf mongoose	*Helogale parvula*
Egyptian mongoose (Ichneumon)	*Herpestes ichneumon*
Flat-headed cusimanse	*Crossarchus platycephalus*
Gambian mongoose	*Mungos gambianus*
Meerkat	*Suricata suricatta*
Somali dwarf mongoose	*Helogale hirtula*
White-tailed mongoose	*Ichneumia albicauda*

Pigs (Suidae)

Giant forest hog	*Hylochoerus meinertzhageni*
Warthog	*Phacochoerus africanus*

AVES

African marsh harrier	*Circus ranivorus*
Marabou stork	*Leptoptilos crumeniferus*
Martial eagle	*Polemaetus bellicosus*
Yellow-billed kite	*Milvus aegyptius*

REPTILIA

African rock python	*Python sebae*
Monitor lizard	*Varanus niloticus*

INVERTEBRATA

House-hunting ant	*Leptothorax albipennis*

CHAPTER 1

Variable leadership in cooperatively breeding banded mongooses is influenced by reproductive state

to be submitted

Variable leadership in cooperatively breeding banded mongooses is influenced by reproductive state

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ABSTRACT

To preserve the advantages of group living, social animals need to maintain group cohesion. This requires that individuals make consensus decisions about the timing of mutually exclusive activities, allowing synchronized behaviors such as moving together and foraging socially. As individuals may show different foraging efficiencies and energetic needs and possess different information on where to find specific resources, it is essential to understand what factors affect leadership in travel decisions. We studied initiation of group departure in the cooperatively breeding banded mongooses (*Mungos mungo*). We investigated how age, sex and the reproductive state of an individual influence its frequency to attempt the initiation of group departure. Moreover, we investigated how age, sex and the production of specific moving calls influenced the success of initiation attempts. We found that leadership in group departure was highly variable, and neither influenced by sex nor by age of individuals overall. However, during periods of synchronized breeding, lactating females initiated group departure more often than expected by chance. Our results suggest that in banded mongooses the variable leadership in initiating group departure is influenced more by reproductive state of an individual, potentially due to energetic constraints, rather than its age or sex. Moreover, the success of initiation attempts seemed to be affected by the production of moving calls of followers. Thus, the success of an initiator's attempt to lead group departure appears to depend on 'acoustic votes' of followers.

INTRODUCTION

For many social animal species, the ability to maintain group cohesion among individuals is crucial to preserve the advantages of group living (Alexander 1974; Krause & Ruxton 2002), such as the increased likelihood of finding food or detecting predators (Pulliam & Caraco 1984, Giraldeau & Caraco 2000). To synchronize activities, individuals of a group need to make decisions through a 'consensus' process; otherwise, the group will split apart (Conradt & Roper 2005). Individuals, however, may differ in their foraging efficiencies, energetic needs and/or information about the environment and thus conflicts of interest about the timing of mutually exclusive activities, such as foraging and resting, might arise (Conradt & Roper 2003; Kerth et al. 2006). Moreover, in some species only very few group members possess the information on where to find certain important resources (Franks et al. 2002; Seeley 2003). Therefore, it is essential to understand how individual differences influence consensus decision-making.

Groups and societies of animals vary in the extent to which certain individuals are consistent leaders in group decisions (Leca et al. 2003). In stable social groups, 'consistent leadership' occurs when a particular group member (usually the most dominant) leads group movements (Conradt & Roper 2005, e.g. dominant individual Boinski 2000; Byrne 2000), whereas 'variable leadership' (Conradt & Roper 2005) occurs when different individuals make decisions on different occasions, and dominant individuals share leadership with subordinate individuals (Leca et al. 2003). In these latter cases, whether dominant individuals lack the ability to enforce decisions or just may not benefit from doing so, is poorly understood (Conradt & Roper 2003; Turbé 2006). Furthermore, it has been suggested that in closely related primate species, social organization influences leadership processes. For example, in some primate species where females are the dominant sex, they are responsible for the travelling choices, whereas in species characterized by the absence of female dominance over males variable leadership occur (Erhart & Overdorff 1999; Jacobs et al. 2008; Sueur & Petit 2008).

The influence of dominance on leadership in stable social groups with consistent leadership however might be overrated. In mountain gorillas (*Gorilla gorilla beringei*), for example, the dominant male is often also one of the oldest and most experienced group members (Schaller 1963; Stewart & Harcourt 1994). Thus, it remains unclear whether the social status or the age

is most important (Turbé 2006). Furthermore, another confounding factor might be the energetic needs of dominant individuals. In dwarf mongooses (*Helogale parvula*), the dominant female appears to make all movement decisions (Rasa 1987). However, as the dominant female is also the sole breeder in the group (Creel & Creel 1991) her energy-consuming reproductive activity may make her the hungriest individual. In plains zebra (*Equus burchelli)*, lactation plays a key role in leadership, suggesting that during lactation early access to certain resources may influence the motivation of movement initiation (Fischhoff et al. 2007). In line with these findings, Rands et al. (2003) state that particular decisions might be initiated by the individual with the strongest need for change at that time. Game-theoretical models of a pair of animals predict that the individual with lower energetic reserves should emerge as the leader who determines when the pair should forage as it gains more from the first move than the other group member (Rands et al. 2003; Cant & Shen 2006). If we are to better understand leadership in group departure it is crucial to take an integrated approach to assess which, if any, of the aforementioned factors play important contributing roles.

We analysed leadership in group decisions by focusing on the initiation of morning group departure from their overnight dens in banded mongooses (*Mungos mungo*). Banded mongooses are small, cooperatively breeding carnivores that live in stable groups (Cant 2003) with little or no reproductive skew among females (Cant 2000). Multiple females breed in synchrony and all breeding females usually give birth on the same day (Cant 2000). Banded mongooses are diurnal and emerge from their communal overnight den after dawn and leave the den area to forage shortly after. At and just after the onset of movement, often the initiator and followers emit specific 'moving calls' (Figure 1; Roman Furrer, personal observation). As the whole group departs 'en masse' banded mongooses provide a unique opportunity to study factors influencing leadership in group departure among many individuals in a low-skew society.

In this study, we investigated the effects of identity and reproductive state on the likelihood to initiate group departure and the success in doing so. In particular, we analysed whether age, sex and reproductive state influenced the frequency of initiation attempts of individuals, and how age, sex and the production of moving calls influenced the success in initiating group departure. We predicted that in cooperatively breeding banded mongooses, in which females exhibit low reproductive skew (Cant 2000) and lack a clear linear dominance hierarchy,

initiation of group departure would be variable and influenced by the female reproductive state during synchronized breeding periods.

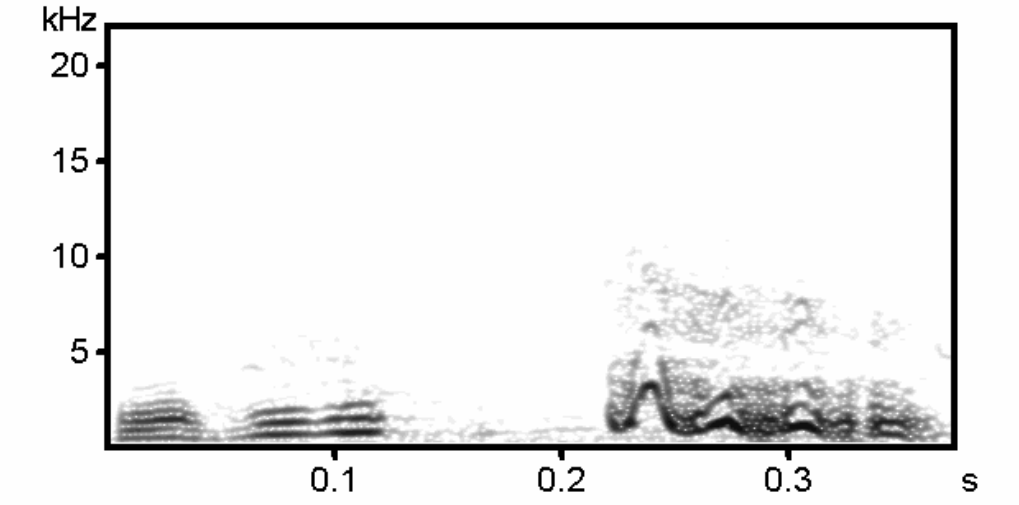

Figure 1. Spectrogram of a moving call (consisting typically of two elements) produced during group departure by initiators and/or followers of an initiation attempt. Spectrogram parameters: frequency resolution; FFT length 512, frame size 75%, window Gauss 3.0, temporal resolution; overlap 93.75 %.

METHODS

Study site and animals

Data were collected from July 2006 to November 2007 on a wild but habituated population of banded mongooses living on and around Mweya Peninsula, Queen Elizabeth National Park, Uganda (0°12'S; 29°54'E). The vegetation of the study site was mainly short grassland interspersed with numerous dense thickets (for details of the study area see Cant 2000; De Luca & Ginsberg 2001). During this study, the population consisted of 142 adult individuals in six groups, ranging from 7 to 44 individuals per group allowing close-range observations. Animals were classified as adults (>12 months), sub-adults (6-12 months), juveniles (3-6 months) and pups (<3 months). For individual identification, all individuals were trapped on a regular basis. Adults were fitted with color coded plastic collars. Sub-adults and infants were marked by shaving a small area of fur of the rump and pups were individually marked by coloring small areas of fur with hair-dye. Trapping and marking procedures followed the guidelines of the Association for the Study of Animal Behavior and are described in detail elsewhere (Cant 2000; Hodge 2007).

Behavioral observations

Data on leadership in group departure from the den was collected by two observers in six social groups on 412 mornings (range: 40 to 102 days per group). To localize the group, we radio-tracked them in the late afternoon and followed them until they went into the den around sunset. On the following morning we waited beside the den until individuals emerged. As part of a long term project, individuals were weighed with a portable electronic balance (Sartorius BL3) after emerging from the den (cf Hodge 2005; Hodge 2007). This allowed us to collect data on weight gain to confirm the reproductive status of the females. After weighing the individuals, they stayed closely together until an individual initiated group departure by moving away from the den area (at least ten meters away from the den in any direction). An attempt to initiate group departure was defined as 'successful' if the initiator was followed by the other individuals. In rare cases, initiation attempts were also classified as successful when two individuals initiated group movement at the same time, moving in different directions and followers split up staying with the initial leader for at least ten minutes. We defined an initiation attempt as 'not successful' if the initiator was not followed, if followers moved back to the den area or followed shortly but then moved away and followed another initiator moving in another direction.

Analyses

To obtain data on leadership of group departure we observed 503 initiation attempts. In 84 initiation attempts we could not identify the initiator of group movement. Out of the remaining 419 successful and not successful initiation attempts, only eight (1.9 %) were led by sub-adults. Subsequently, we excluded these eight initiation attempts and analysed the 411 initiation attempts made by adult individuals.

To investigate how often individuals tried to initiate group movement we calculated an initiation attempts ratio. It was calculated by adding successful and not successful initiation attempts of each adult individual and divided the total by the number of all adult initiation attempts occurring in its group when the focal individual was present. The initiation attempts ratio, was calculated for all adult individuals. We then investigated the influence of sex, relative age (i.e. whether an individual belongs to the older or the younger half of all adult group members at the time the initiation attempt occurred) and age ranks on the initiation attempts ratio.

During periods of synchronized pregnancy and lactation we tested whether the observed frequency of initiation attempts made by individuals of a particular reproductive status differed from the frequency expected by chance. To do so, we firstly noted the sex and for females the reproductive state of the initiator and counted the number of individuals present of each reproductive state (reproductive female, non-reproductive adult female, adult male). Secondly, we determined the total number of initiations of individuals of a particular reproductive state and counted the total number of all individuals present of a certain reproductive state during all initiation attempts within that group. We then calculated the observed and the expected percentages of initiation attempts for each of the reproductive states within the six social groups. During the gestation period (approximately 60 days), pregnancy becomes evident from around the fourth week of gestation, as females have visibly swollen bellies (Gilchrist 2001) and gain weight. Hence, we analysed data from the last four weeks of pregnancy and assigned, after each initiation attempt, the reproductive state of the initiator and the number of pregnant-, non-pregnant females and males present. For initiation attempts occurring during periods of lactation, we determined the number of lactating females within the group by direct observation of females suckling pups and by investigating trapped and anaesthetized females. We analysed data derived from periods of lactation from the first six weeks after females had given birth. Data from periods in which particular females were still lactating (within the first six weeks of lactation), but already clearly pregnant again, were omitted. We did not analyse data collected during the few periods of non-synchronized breeding when some females were pregnant and others were lactating.

To investigate how successful individuals were in initiating group departure we calculated an initiation success ratio. It was calculated for each adult individual that at least once attempted to initiate group departure. We divided all successful initiation attempts of a focal individual by the total number of initiation attempts of that individual. We then analysed the influence of sex, relative age, the proportion of initiation attempts during which the focal initiator emitted moving calls, and the proportion of initiation attempts during which at least another individual emitted moving calls at the onset of the initiation attempt (within the first five seconds after the initiator started to move) on the initiation success ratio.

Statistical analyses

Statistical tests were performed using R 2.7.1 (R Development Core Team 2008). To analyse factors that might affect an individual's frequency and success in initiating group departure we

carried out generalised linear mixed-effect models (GLMMs) with quasibinomial error structure and logit-link function. To analyse the initiation success ratio we conducted a weighted GLMM controlling for the different number of observed initiation attempts among group members. We controlled for the repeated sampling of the same group with 'group' fitted as a random factor (Crawley 2002) using the packages lme4 (Bates et al. 2008) and MASS (Venables & Ripley 2002). Non-significant factors were omitted from the final models (Crawley 2002). All interactions were non-significant and were thus omitted from the final models (Engqvist 2005). From the resulting F-values we calculated the *P*-values according to Faraway (2005). To investigate whether the age ranks of the adult individuals correlated with their initiation attempts ratio and their initiation success ratio within the six social groups, we conducted Spearman rank correlations. Individuals born on the same day were assigned age ranks randomly within their age range. We analysed the influence of the different reproductive states on initiation attempts by comparing the observed percentages of initiation attempts of individuals of a particular reproductive state with their expected percentages of initiation attempts according to their frequency within the social group. Because data were not normally distributed we used exact Wilcoxon signed-ranks tests (Sokal & Rohlf 1995; Mundry & Fischer 1998).

RESULTS

Initiation attempts overall

Leadership in group departure was highly variable with 103 out of 142 (73 %) adult individuals initiating group movement at least once. Overall, the initiation attempts ratio was not influenced by the relative age of an individual (GLMM: $F_{1,139} = 1.6$, $P = 0.2$). Within the six groups, the age ranks of the adult individuals correlated only in one group with their initiation attempts ratio (group D: $r_s = 0.54$, N = 28, $P = 0.003$; group B: $r_s = 0.28$, N = 33, $P = 0.12$; group F: $r_s = 0.12$, N = 27, $P = 0.54$; group H: $r_s = -0.25$, N = 29, $P = 0.19$; group S: $r_s = 0.05$, N = 9, $P = 0.9$; group V: $r_s = 0.38$, N = 16, $P = 0.18$). The initiation attempts ratio was not influenced by the sex of an individual (GLMM: $F_{1,139} = 2.6$, $P = 0.11$).

Initiation attempts during periods of pregnancy and lactation

The initiation attempts of females, however, were influenced by their reproductive state. During synchronized breeding attempts, pregnant females tended to initiate group departure

more often than expected (exact Wilcoxon signed-ranks test: N = 6, T^+ = 19, *P* = 0.094) whereas non-pregnant females did not initiate group departure more often than expected (N = 6, T^+ = 9, *P* = 0.787). Males tended to initiate group departure less often than expected (N = 6, T^+ = 1, *P* = 0.063; Figure 2). During periods of synchronized lactation lactating females initiated group departure more often than expected (exact Wilcoxon signed-ranks test: N = 6, T^+ = 21, *P* = 0.031) whereas non-lactating females did not initiate more often than expected (N = 6, T^+ = 6, *P* = 0.787) and males initiated less often than expected (N = 6, T^+ = 0, *P* = 0.031; Figure 3).

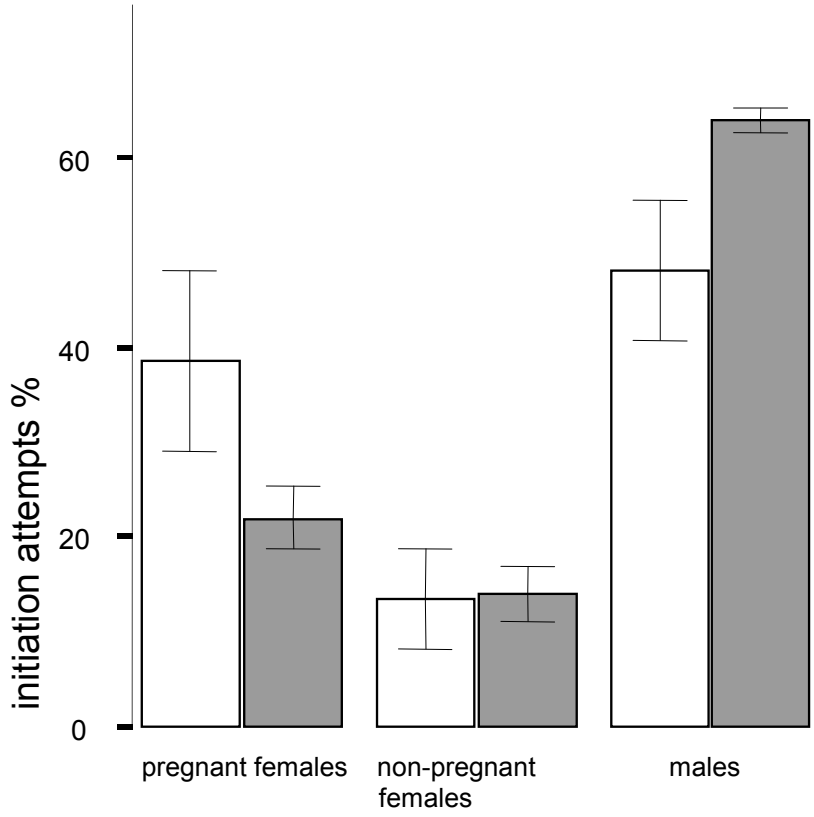

Figure 2. Mean ± SE percentages of initiation attempts during periods of synchronized pregnancy of pregnant-, non-pregnant females and males (means of 6 groups, derived from 95 initiation attempts). The white bars represent the observed percentages of initiation attempts whereas the grey bars show the expected percentages of initiation attempts according to the frequencies of occurrence within the six social groups.

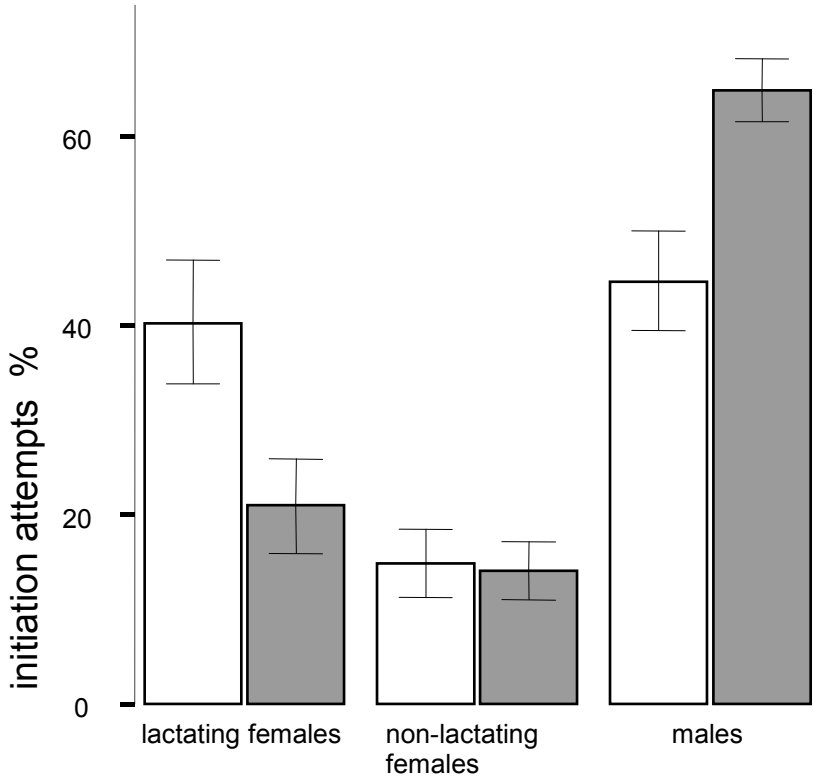

Figure 3. Mean ± SE percentages of initiation attempts during periods of synchronized lactation of lactating-, non-lactating females and males (means of 6 groups, derived from 129 initiation attempts). The white bars represent the observed percentages of initiation attempts whereas the grey bars show the expected percentages of initiation attempts according to the frequencies of occurrence within the six social groups.

Initiation success

The success of initiating group departure was influenced by the vocal behavior of followers and the sex of initiating individuals. The proportion of initiation attempts during which at least one other individual emitted moving calls at the onset of the initiation attempt influenced the initiation success ratio (GLMM: $F_{1,100} = 11.97$, $P < 0.001$; Figure 4). Individuals with a higher proportion of being accompanied by other individuals calling were more successful in initiating group departure. Sex tended to have an effect on the initiation success ratio (GLMM: $F_{1,100} = 2.9$, $P = 0.091$; Figure 5) with females showing higher initiation success than males. Overall, the relative age did not influence the initiation success ratio (GLMM: $F_{1,100} = 0.002$, $P = 0.96$) and within the six social groups, the age ranks of the adult individuals correlated only in one group with their initiation success ratio (group B: $r_s = 0.47$,

N = 24, $P = 0.021$; group D: $r_s = -0.15$, N = 18, $P = 0.55$; group F: $r_s = -0.28$, N = 15, $P = 0.3$; group H: $r_s = -0.28$, N = 24, $P = 0.19$; group S: $r_s = -0.062$, N = 8, $P = 0.88$; group V: $r_s = 0.19$, N = 14, $P = 0.53$). Finally, the proportion of initiation attempts during which the focal initiator emitted moving calls (GLMM: $F_{1,100} = 0.076$, $P = 0.78$) did not influence the initiators' success in initiating group departure.

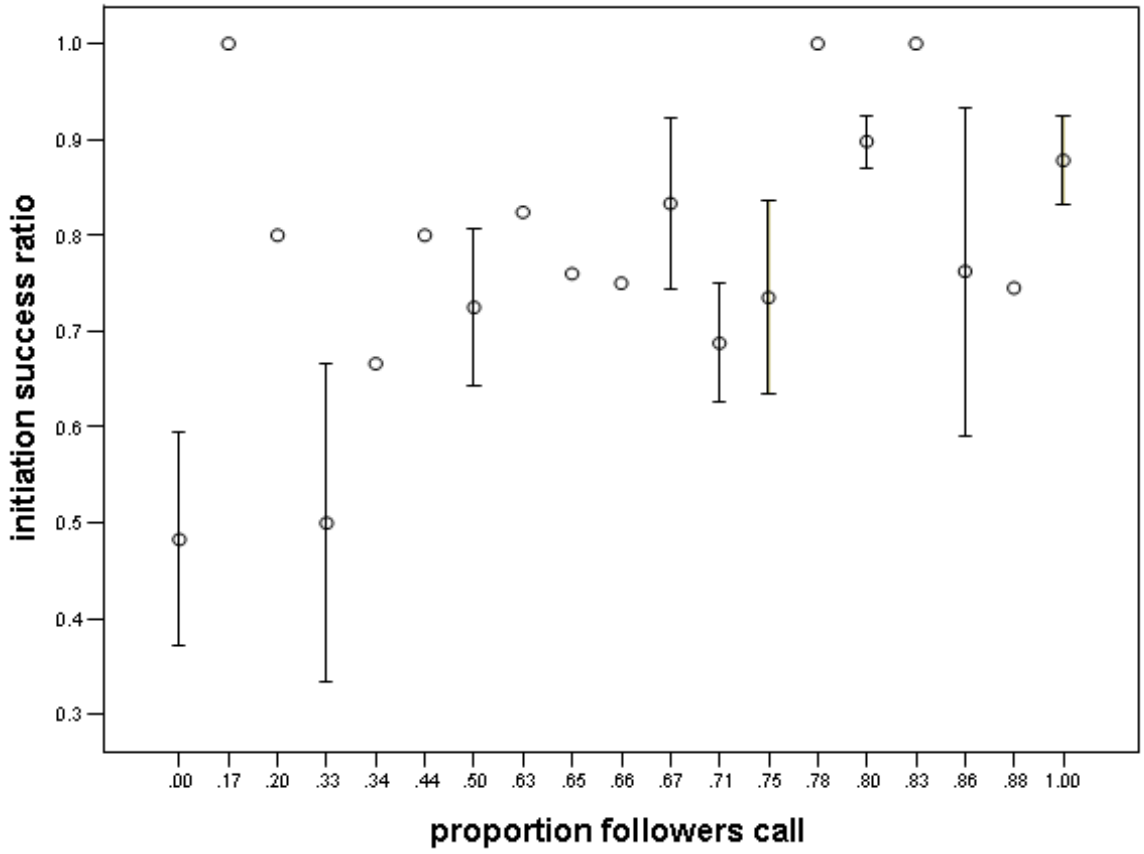

Figure 4. The influence of the proportion of initiation attempts during which at least one follower emitted moving calls (proportion followers call) on the initiation success ratio of initiators (mean ± SE).

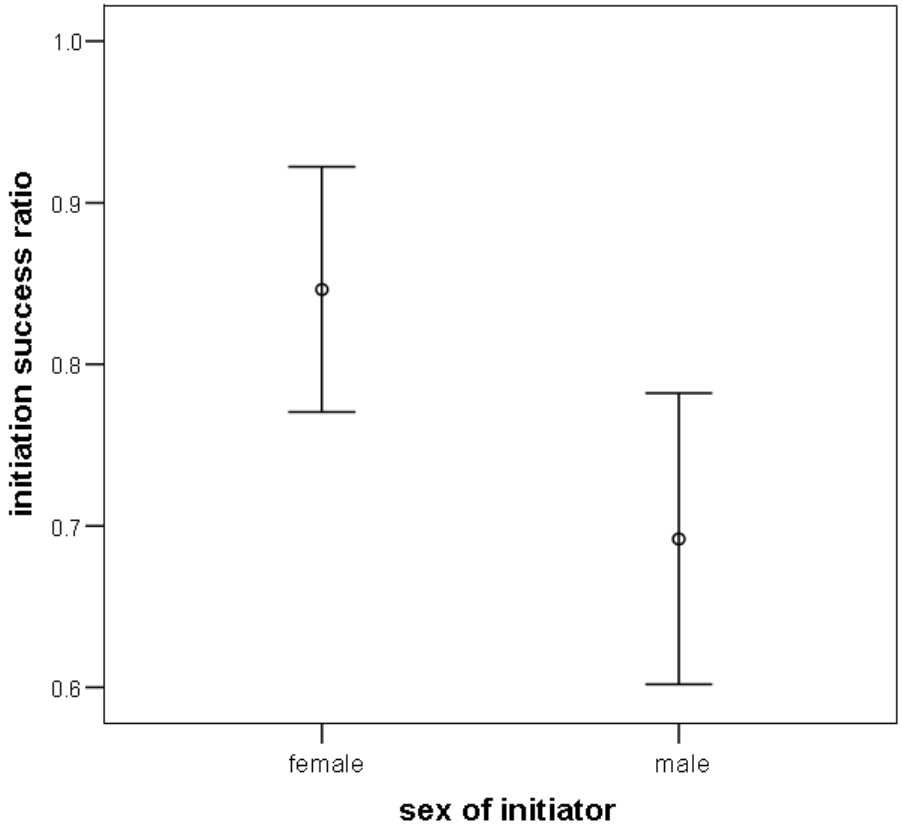

Figure 5. The influence of the initiator's sex on the initiation success ratio of initiators (mean ± SE; females: N = 42; males: N = 61).

DISCUSSION

In banded mongooses leadership in group departure from the den was highly variable. More than seventy percent of the adult individuals attempted to initiate group departure at least once. The likelihood to initiate group departure did not differ between females and males and did not seem to be influenced by the relative age of the adult individuals. Out of the six social groups, only one group showed a correlation between the age ranks of the adult individuals and their likelihood to initiate group departure. Similarly high percentages of group members involved in initiation of group movement have been shown in studies on free ranging and semi-free ranging primates (Leca et al. 2003; Jacobs et al. 2008; Stueckle & Zinner 2008). It has been suggested that the degree of variability in leadership of group departure might be influenced by the species' social organization (Jacobs et al. 2008). In lemur species, where females are dominant over males, females were primarily responsible for the time and direction of departures (Erhart & Overdorff 1999). In another lemur species with no female dominance, leadership was distributed amongst all group members (Jacobs et al. 2008). In

line with these results from primate studies, the social system might also influence leadership in different mongoose species. In dwarf mongooses, travel decisions are made by the dominant female (Rasa 1987), whereas our data, collected in a low-skew society with no dominant breeding pair, show that neither a particular group member nor a group of certain individuals monopolized initiation of group departure overall.

However, during periods of synchronized breeding, pregnant female banded mongooses tended to initiate group departure more often than expected and lactating females initiated more often than expected compared to their occurrence within the social groups. These results suggest that female reproductive state and lactation in particular, had an influence on leadership of group departure. Thus, in closely related dwarf mongooses, where the dominant female produces several litters a year (Creel & Creel 1991), consistent leadership in travel decisions by dominant females might be influenced more by their energy-consuming reproductive activity than their dominance status. The influence of the reproductive state on leadership is also supported by high-skew, seasonally breeding meerkats *(Suricata suricatta)* where the dominant female typically is the sole breeder in the group (Clutton-Brock et al. 2001). During lactation, the dominant females initiated over four times as many departure attempts compared to the non-breeding season (Turbé 2006). These findings suggest that, independent of the degree of reproductive skew among females, the reproductive state, particularly lactation, appear to have a greater influence on the initiation of group departure than the species' social organization.

Lactation provides females and their offspring independence from potential short-term fluctuations in food supplies. However, as converting food into milk is relatively inefficient at delivering nutrients to young (Dall & Boyd 2004) it is plausible that lactating females become heavily involved in leadership of group movement due to their increased energetic need (Rands et al. 2003). By using game-theoretical models Rands et al. (2003) suggested that in pair of foraging animals the individual with lower energetic reserves should emerge as pace-maker and determine when to forage. Although evidence that individuals with low energetic reserves may act as pace-makers was found in salmon (*Salmo salar*, Gotceitas & Godin 1991) and roach (*Rutilus rutilus,* Krause et al. 1992) it is still ambiguous whether energetic reserves are important for decision-making in social foragers (Rands et al. 2008). Furthermore, 'leading according to need' was described for self-organising groups, where individuals follow local behavioral rules, resulting in organised behavior of the group without the need for global

control (Conradt & Roper 2005). Here, group movements are likely to be led by individuals for which reaching a specific destination is most crucial or group cohesion is least important (Conradt et al. 2009).

Without accounting for data on foraging success of group departure initiators we cannot clearly link leadership with low energetic resources. However, in banded mongooses, the reproductive state of the females appeared to have a major impact on leadership of group departure. As Cant (2000) showed among adult females there is no difference in the proportion of females becoming pregnant between age classes, it is likely that in banded mongooses the reproductive state of the female and not the age affects the likelihood to initiate group departure. Additional studies have shown that in some species only a few individuals may posses the information about where to find important resources (Franks et al. 2002; Seeley 2003). Banded mongooses however, search and dig for invertebrate and small vertebrate prey (Rood 1975) which is not bound to just a few locations in their relatively small home ranges (average home range size: 90.5 ha; cf Gilchrist & Otali 2002). For banded mongooses, the degree of information about important resources might not vary that much among group members. Therefore, the reproductive state (potentially due to energetic constraints) and not the identity appear to have a major impact on the likelihood to initiate group departure.

In banded mongooses, acoustic cues played an important role in the success of initiation attempts. Initiators with a high proportion of being accompanied by at least another group member producing moving calls showed higher success in leading the group away from the overnight den. In a variety of species, specific vocalizations appear to accompany the initiation of group movement (Boinski 1991; Boinski et al. 1994). In primates, specific vocalizations are associated with the initiation of movement of a stationary group in a specific direction (e.g. white-faced capuchins *(Cebus capucinus)*, Boinski & Campbell 1995), with vocalizations being produced by both leaders and followers at high rates during group progressions (e.g. Verreaux's sifakas *(Propithecus verreauxi)*, Trillmich et al. 2004). In group-living green woodhoopoes (*Phoeniculus purpureus*), an individual moving to a new foraging site is more likely to be followed if it vocalizes rather than if it remains silent (Radford 2004). In banded mongooses however, for the success of the attempt, the calls of other individuals during group departure seem to be more influential than the calls of the initiator. Thus, some

acoustic ‘votes’ (see Conradt & Roper 2005) of followers during departure may play a crucial role in successfully recruiting the rest of the group members.

Besides calling during the initiation attempt, acoustic or visual behaviors produced prior to group departure (Kummer 1968; Stolba 1979; Stewart & Harcourt 1994) could also influence the success of the initiation attempts. However, neither acoustic nor visual pre-move signals were obvious in banded mongooses (R. Furrer, personal observation). Furthermore, in banded mongooses, females tended to show a higher initiation success ratio than males. Whether females produce moving calls that differ from the ones of males in parameters, such as acoustic structure, amplitude or call rate still needs to be tested. Moreover, during oestrous periods, receptive females are followed by mate-guarding males typically throughout the foraging trips (Cant 2000). To monitor the females' activities, males could pay more attention to adult females than to males and offspring even outside receptive periods, which may influence the success of the females' initiation attempts. This effect could be further amplified by the commonly male-biased sex ratio among adults of the study population groups (De Luca & Ginsberg 2001; Gilchrist 2001).

In summary, initiation of group departure in banded mongooses was highly variable but influenced by the reproductive state of females during periods of synchronized breeding. During lactation when energetic needs of females are high, the likelihood of lactating females to initiate group departure was higher than expected. Consequently, the energetic state of an individual rather than its identity might have a stronger influence on leadership in initiation of group departure. Females tended to be more successful in initiating group departure and the success of initiation attempts was influenced by acoustic votes of other group members during the onset of group travel. The success of a single individuals' decision to try to initiate group departure therefore appears to depend on the acoustic responses of followers.

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CHAPTER 2

The influence of nutritional constraints on leadership roles in banded mongooses

to be submitted

The influence of nutritional constraints on leadership roles in banded mongooses

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ABSTRACT

As many animal species benefit from living in groups, communal decisions about when to forage and where to go, need to be made to prevent the group from splitting apart. While in some species particular individuals or subgroups emerge as consistent leaders in movement decisions, in others many different individuals initiate coordinated group movements. Game-models suggest that in a pair of foraging animals, state-dependent variable leadership should occur. Here, the individual with lower energetic reserves should spontaneously emerge as the leader determining when to forage. We analysed whether in banded mongooses (*Mungos mungo*), a species where leadership in group departure is highly variable, nutritional constraints influenced leadership roles. Results from deprivation of food/feeding experiments revealed that initiators of group departure tended to be deprived individuals suggesting that low energetic reserves caused by bad foraging success can have an influence the individuals' likelihood to act as initiators. However, analysis of weight data showed that initiators did not have a lower body weight compared to when not initiating. These findings indicate that apart from short-term foraging success, other factors also appear to be important in determining leadership. Such key determinants could be high energetic demands during periods of lactation, asymmetries in foraging abilities or differences in the time available for foraging due to variable investment in cooperative activities between individuals. Thus, we conclude that while nutritional constraints can influence initiation of group departure in banded mongooses, effects of individual differences may equally affect leadership roles.

INTRODUCTION

Many animal species forage and travel in groups (Krause & Ruxton 2002). Forming groups might help to gain protection from predators, improve breeding, exchange information and compete against rivals (Alexander 1974; Vanschaik 1983; Richner & Heeb 1995). To preserve these group advantages, social animals need to maintain group cohesion (Alexander 1974; Krause & Ruxton 2002) which can be achieved through the process of consensus decision making. Here, group members choose between two or more mutually exclusive actions with the aim of reaching a consensus (Seeley et al. 1999; Conradt & Roper 2005). In small groups, where individuals can communicate globally (i.e. with all other group members, Conradt & Roper 2005), often an individual acts as 'leader' or 'initiator' of coordinated group movement. In some species, certain individuals consistently lead group movements (Kummer 1968; Dunbar 1983; Dumont et al. 2005) whereas in other species various individuals initiate such activities (Lamprecht 1992; Leca et al. 2003; Radford 2004). While consistent leadership in group movement might be influenced by the knowledge of experienced individuals about the location of food sources (Reebs 2000; Swaney et al. 2001), the species' social organization (e.g. influence of social dominance: Schaller 1963; Erhart and Overdorff 1999; Jacobs et al. 2008; Sueur and Petit 2008) and personality characteristics (Ward et al. 2004; Leblond & Reebs 2006; Harcourt et al. 2009; Kruvers et al. 2009), little is known about what may cause variable leadership. Fischhoff and colleagues (2007) showed that in plains zebra (*Equus burchellii*) the reproductive state was a key determinant of variable leadership. Lactating females, with high energetic requirements, were more likely to initiate group movement than non-lactating females. Rands and colleagues (2003) noted by developing a state-dependent game model that in a pair of foraging animals, if there is an advantage of foraging together, the behaviour of both individuals becomes highly synchronized. As a result of this synchronization, differences in energetic reserves of the two animals develop, resulting in different behavioural roles for each of the two. The individual with lower reserves emerges as the temporary leader deciding when the pair should forage (Rands et al. 2003). Studies of foraging fish showed that individuals with lower reserves often occupy front positions in schools (Goceitas & Godin 1991; Krause et al. 1992; Krause 1993; Krause et al. 1998). However, evidence is still ambiguous for whether energetic reserves are important for decision-making in social foragers (Rands et al. 2008). Furthermore, if one considers possible differences such as metabolic requirements between the pair members, the adoptions of behavioural roles are even more complex for the two animals (Rands et al. 2008). Dynamic

game models involving two animals only present a first step in trying to explain leadership roles of larger groups. Nevertheless, such models can produce meaningful predictions that are testable (Thomas 2000; Rands & Cuthill 2001; Rands et al. 2008).

In this study we investigated whether low energetic reserves may influence the leadership roles in group departure of banded mongooses (*Mungos mungo)*. Banded mongooses are small, cooperatively breeding carnivores that live in stable, mixed-sex groups (Cant 2003) with little or no reproductive skew among females (Cant 2000). Groups breed up to five times per year and often multiple females breed in synchrony and all breeding females usually give birth on the same day (Cant 2000). After emerging from the overnight den the whole group departs 'en masse' with individuals moving in an orderly file, either single or up to three animals abreast. When foraging, group members are more spread out but group cohesion is always maintained and aided by contact calls (Rood 1975). In a related study, we showed that in banded mongooses leadership in group departure is highly variable and the likelihood to initiate group departure is neither influenced by the sex nor by the age of the individuals overall (chapter 1). As such, banded mongooses provide an excellent opportunity to analyse whether in relatively small stable social groups, where individuals can communicate globally (Conradt & Roper 2005), variable leadership in group departure might be influenced by nutritional constraints. We addressed this in the present study by analyzing whether an initiator's weight was relatively low in comparison to the same individual's weight taken on non-initiating days. Furthermore, with short-term deprivation of food/feeding experiments, we tested whether low energetic reserves caused by bad foraging success may influence the likelihood to initiate group movement. If initiation of group departure might be influenced by bad foraging success we would firstly expect initiators to have a lower weight compared to periods when they are not initiating. Secondly, we expected that individuals being experimentally deprived of food would initiate group departure on the following morning.

METHODS

Study Site and Animals

This study was carried out on a wild population of banded mongooses living on and around Mweya Peninsula, Queen Elizabeth National Park, Uganda (0°12'S; 29°54'E; for details of the study area see Cant 2000; De Luca and Ginsberg 2001). Weight data of initiators of group

departure were collected from July 2006 to November 2007 and experiments with short-term deprivation of food were conducted form May to December 2007. The study population consisted of six groups of habituated banded mongooses ranging from 7 to 44 individuals that allowed close-range observations and weighing of individuals in the field. Animals were classified as adults (>12 months), sub-adults (6-12 months), juveniles (3-6 months) and pups (<3 months). For individual identification, adults were fitted with colour coded plastic collars. Sub-adults and infants were marked by shaving a small area of fur of the rump, and pups were individually marked by colouring small areas of fur with blonde hair-dye (see Cant 2000; Hodge 2007 for descriptions of trapping and marking techniques). Trapping and experiments were conducted in accordance with ASAB/ABS guidelines for the use of animals in research.

Weighing Methods

As part of a long term project individuals have been habituated to be weighed in the field (see Hodge 2005; Hodge 2007). In the morning after the individuals emerged they were weighed with a portable electronic balance (Sartorius BL3) near to their den. Individuals were attracted to the spot where weights were taken by distributing a small quantity of bait in form of a few rice corns with gravy on the ground. In response to a reward of a drop of cow milk put in the portable balance individuals either stepped themselves or were lifted onto it. While licking the milk, individuals remained calm and weights could be read without fluctuations. With few exceptions, adult individuals were weighed regularly and their offspring were habituated to be weighed. The whole weighing process lasted normally between 2 and 15 minutes depending on the group's size.

Analysis of Weight Data of Initiators

After weighing, individuals stayed closely together near the den until an individual initiated group departure by moving away from the den area (at least ten meters away from the den in any direction; see chapter 1). To analyse whether foraging success may influence the likelihood to initiate group departure we compared the weight of an initiator (w_{ini}) with its morning weight from the previous day ($w_{iniprev}$) and calculated a weight balance (b_{ini}):

$$w_{ini} - w_{iniprev} = b_{ini}$$

The weight balance of an initiator (b_{ini}) was only calculated if it did not initiate group departure on the previous day ($w_{iniprev}$). We then compared the weight balance of an initiator

of group departure (b_{ini}) with its weight balance calculated from 2 days in succession in which this individual did not initiate group departure (b_{cont}):

$w_{cont} - w_{contprev} = b_{cont}$

In males, the control weight balance (b_{cont}) was calculated from the next period in which weights of an initiator were collected during which this individual did not initiate group departure on both days. In addition, in females, the control weight balance (b_{cont}) was calculated from the next period in which weights of an initiator were collected in the same reproductive state (pregnancy, lactation, non-reproductive but adult). For each individual, we analysed the first initiation attempt in which weights were collected. Furthermore, in females, we also analysed their first initiation attempt observed during the three reproductive states if data were available. We chose not to compare the weight of the initiator with the individual's average weight as seasonal food availability and differences in female reproductive state may influence an individual's body weight. Instead, comparing weights in a short time frame, would address the constraints mentioned above. If a bad foraging success influenced the likelihood of initiating group departure on the following day we expected that the weight balance taken from the period in which an individual acted as initiator (b_{ini}) would be more negative than the control weight balance taken from a period in which this individual did not initiate group departure (b_{cont}).

Short-term deprivation of food/feeding experiment

To test whether nutritional constraints caused by bad foraging success may influence the likelihood to initiate group departure we carried out short-term deprivation of food/feeding experiments. We analysed whether individuals that were deprived of food in the afternoon were more likely to initiate group departure on the following morning than individuals that were fed by the observers. To account for differences in the foraging abilities among individuals we captured all individuals taking part in the experiment and fed half of them while the other half was deprived of food. All individuals were captured in the afternoon around 2.30 pm and released in the evening near the den around 7 pm (as the study site lies just about 20 km south of the equator the day length does not change substantially and it is getting dark always a few minutes after 7 pm). As less than 2% of the observed initiation attempts were undertaken by non-adults (chapter 1) only adult individuals were captured for the experiment. We captured individuals using box traps (67 x 23 x 23 cm; Tomahawk Live

Trap Co.). We did not capture the individual that was fitted with a refurbished Sirtrack® radiocollar (Sirtrack, Havelock North, New Zealand) and few other adults to stay with the offspring. Trapped individuals were carried to a nearby vehicle and driven to the laboratory, where individuals were then transferred to a cloth bag until fully anaesthetized to minimize stress (see Jordan et al. in press for details on trapping techniques). For individual identification, we replaced the individuals' color-coded plastic collars in adults and shaved a small area of fur of the rump in subadults during anaesthetization. After this about five min lasting process, individuals were placed back into the trap. Traps were covered by fabric and water to drink was provided inside. Afterwards half of the captured group members were fed and the other half was deprived of food in alternative order according their age. To know how much food should be provided, we measured the weight gain of banded mongooses during afternoon foraging previously. We weighed individuals of the 6 experimental groups around 2.30 pm and again before they went back into den around 7 pm (duration between the measurements: N = 59, mean ± SD; 260.1 min ± 10.7 min). The individual's weight gain ranged between -22 g and + 68 g (N = 59, mean ± SD; 23.8 g ± 22.8 g). Thus, we simulated a good afternoon foraging success by providing 50 gram of fried egg for the individuals that were to be fed. To account for different energetic requirements among females we did not conduct the experiment when females were in the later stages of pregnancy or lactating. Afterwards we radio-tracked the individuals, which had not been captured, and released the captured individuals near the den around 7 pm. We observed the individuals going into the den and stayed near the den for another 15 minutes.

On the following morning we arrived near the den at dawn and waited there until individuals emerged. The identity of the individual initiating group departure by moving away from the den area (at least ten meters away from the den in any direction, see chapter 1) was noted by both observers. We intended to conduct the experiment twice in a paired design in the 6 experimental groups in a way that each captured individual was deprived of food and fed once. After carrying out an experiment we waited at least 3 weeks before conducting another experiment of this type. In 7 cases the experiment could not be analysed and had to be repeated for the following reasons: In 3 cases the initiator of group departure could not be identified by one or both of the observers. In 3 cases an individual that was not captured on the previous afternoon initiated group departure on the following morning. In one case interference with other wild animals did not allow close-range observation of group departure. Out of the intended 12 experiments we were able to conduct 11 as in one group the

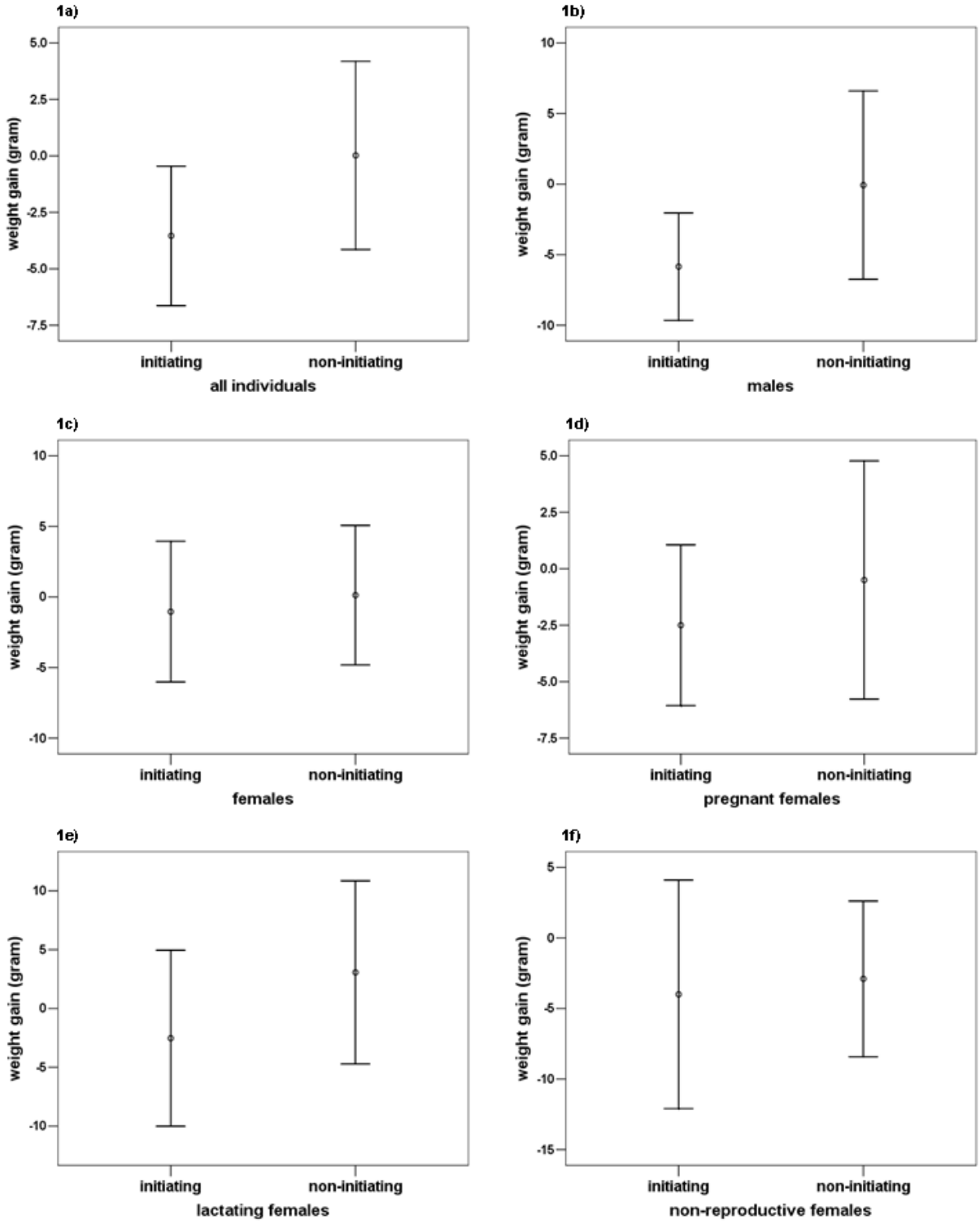
experiment failed 4 times in a row for reasons mentioned above. If nutritional constraints influenced the likelihood to initiate group departure we expected that individuals being deprived of food on the previous day would more often become initiators on the following day.

Statistical Analyses

Statistical tests were performed using R 2.9.1 (R Development Core Team 2009). To analyse the influence of weight gain on the initiation of group departure, we carried out linear mixed-effect models (LMMs). We compared the weight balance of the period in which the focal individual was initiating group departure on the second day with the control weight balance in which the same individual did not initiate group departure on both days in a paired design. In these analyses we controlled for the repeated sampling in the same group with 'group' fitted as a random factor (Crawley 2002) using the packages nlme (Pinheiro et al. 2006) and MASS (Venables & Ripley 2002). To analyse whether individuals that were experimentally deprived of food were more likely to initiate group departure compared to the likelihood in doing so expected by chance we conducted a two-tailed exact binomial test.

RESULTS

The weight balance of the period in which the focal individual was initiating group departure on the second day did not differ in comparison to the control weight balance in which the same individual did not initiate group departure on both days. Overall, the initiators' weight balances of the initiation period were not more negative than the control weight balances (LMM, $N = 50$, estimate ± SE = 3.6 ± 5.2, $t_{49} = 0.69$, $P = 0.5$; Figure 1a). The males' and females' weight balances of the initiation period were not more negative than the weight balances of the control period (males: LMM, $N = 26$, estimate ± SE = 5.8 ± 7.7, $t_{25} = 0.75$, $P = 0.46$; Figure 1b). (females: LMM, $N = 24$, estimate ± SE = 1.2 ± 7, $t_{23} = 0.17$, $P = 0.87$; Figure 1c). When analyzing initiation attempts during certain reproductive states, neither in pregnant females nor in lactating females nor in non-reproductive females the weight balances of the initiation period were significantly more negative than the control balances (pregnant females: LMM, $N = 10$, estimate ± SE = 2 ± 6, $t_9 = 0.34$, $P = 0.75$; Figure 1d; lactating females: LMM, $N = 15$, estimate ± SE = 5.6 ± 10.8, $t_{14} = 0.52$, $P = 0.61$; Figure 1e; non-reproductive females: LMM, $N = 10$, estimate ± SE = -3 ± 10, $t_9 = -0.03$, $P = 0.98$; Figure 1f).



Figures 1a to 1f. The weight of individuals initiating group departure in relation to their weight of the previous day (initiating) compared with weights of a control period in which individuals did not initiate group departure (non-initiating). Shown are mean and standard error.

With deprivation of food/feeding experiments, we tested experimentally whether individuals that were deprived of food in the afternoon initiated group departure more often than fed individuals on the following morning. Deprived individuals tended to initiate group departure more often than fed individuals (Binomial test, $N = 11$. test proportion = 0.5, $P = 0.065$). Group departure was initiated in 9 cases (82 %) by individuals that were deprived of food whereas individuals that were fed by the observers did only so in 2 cases (18%).

DISCUSSION

Our analyses on weight gain of individuals initiating group departure showed that in banded mongooses the initiators' weights in relation to their weight of the previous day were not significantly more negative compared to weights of control periods. In contrast to these findings, the results obtained from the deprivation of food/feeding experiments revealed that deprived individuals tended to be more likely to initiate group departure.

Previous results for banded mongooses show that leadership in group departure was neither concentrated on single individual nor influenced by sex or age with most adult individuals initiating group departure (chapter 1). Contrary to our prediction, the variable leadership in group departure was not influenced by the weight gain of initiators suggesting that the foraging success of the previous day is not the key determinant of leadership roles in banded mongooses. Although pregnant females tended to initiate and lactating females initiated group departure more often than expected (chapter 1) females in these reproductive states did also not show a significantly lower weight when initiating group departure. Studies have shown that during pregnancy and lactation the variability in energetic needs between individuals in a group is highest (Scantlebury et al. 2002) and that lactation is energetically demanding (Dall & Boyd 2004). As reproducing females may have high metabolic requirements throughout pregnancy and lactation, their overall energetic demands appear to be more influential on leadership roles than their short-term foraging success of the previous day. Consequently, individuals with high energetic demands may become pacemakers even while having good energetic reserves. Apart from pregnant and lactating females, non-reproductive females and males also did not show a significantly lower body mass when initiating group departure. For some of these individuals, the time available for foraging might often be limited as in cooperative breeders, where individuals provide care to offspring that are not their own, the

investment in cooperative activities commonly differs among helpers (Cockburn 1998). In banded mongooses, it was shown that contributions to pup care activities are strongly male-biased (Hodge 2007). Until pups are able to forage independently, males contribute more to babysitting and provisioning pups with food items (Rood 1974; Gilchrist 2001; Cant 2003; Gilchrist 2004; Hodge 2005; Hodge 2007). Hence, in anticipation of their significant contribution to pup care during the day males may become pacemakers in determining when and where to forage even when their energy reserves are good. The same argument might apply for non-reproductive females. They may lead the group away from the den independent of their energetic reserves as it was shown that mothers that were not pregnant again provided more food items to foraging but dependent pups than pregnant mothers (Hodge 2007).

Apart from periods of high energetic demands and limited foraging time, asymmetries in foraging abilities among group members may be an important factor as well. Individuals that need more time to forage successfully might become involved in the decision-making of when to leave the den for foraging even while having good energetic reserves. Furthermore, the foraging success of non-initiating group members might also influence leadership. An initiator's weight could be the same or even heavier compared to its weight from the non-initiating previous day but still its weight gain might be relatively low compared to other group members which may have had an even better foraging success on the previous day. Thus, the foraging success of the initiator in relation to the other group members may be an important determining factor. As we generally do not have data on weight gain of all group members taken on two successive days we could not analyse the initiator's weight gain compared to weight gain of all other individuals.

On the contrary, the results obtained from the deprivation of food/feeding experiments revealed that individuals deprived of food tended to be more likely to initiate group departure. In line with the predictions of the game-theoretical model applied for a pair of animals (Rands et al. 2003) energetically needy individuals became pacemakers in social groups of banded mongooses. By feeding half of the captured adult individuals with 50 gram fried egg, we simulated a situation where exactly half of the subjects should have substantially lower energetic reserves. In our experimental design the discrepancy in the foraging success between the two treatment groups was likely to be higher than the differences between individuals occurring naturally. Normally, even individuals that are heavily involved in pup care should find some time to forage for themselves. Hence, leadership roles influenced by

such wide differences in foraging success are not likely to accrue often under natural conditions.

In social animals, synchronization of activities is crucial if the group is to remain spatially coherent (Prins 1996; Conradt & Roper 2003). In small social groups, where group members can communicate globally, individuals lead consensus decisions about group movements (Conradt & Roper 2005). How such leaders emerge is often not well understood (Biro et al. 2006). In banded mongooses, social dominance and personality traits do not seem to influence leadership in group departure. Leadership in group departure is widely shared, social groups lack a clear linear dominance hierarchy and if personality characteristics, such as activity (Beauchamp 2000) or boldness (Ward et al. 2004; Leblond & Rebs 2006) were of importance, leadership should be consistent or a least less variable than observed. Knowledge about important food resources is unlikely to influence their leadership roles as banded mongooses roam all over in their relatively small territories in search of their widely distributed invertebrate and small vertebrate prey (Rood 1975). In large, self-organizing groups, where individuals follow local behavioural rules without global control (Conradt & Roper 2005), group movements are likely to be led by individuals for which reaching a particular destination is most crucial (Conradt & Roper 2009). Although, our results derived from the deprivation of food/feeding experiments provide evidence that 'leading according to need' may also accrue in small groups with global communication, our analysis of weight data did not reveal an influence of short-term weight gain on the likelihood to initiate group departure. Hence, it appears that generally the foraging success of the previous day is not the sole key determinant underlying leadership roles in banded mongooses. Instead, factors like consistent high energetic demands during reproductive periods, asymmetries between individuals in their foraging efficiency and their time available for foraging, as well as the initiator's foraging success in relation to other group members may often be as influential as individual low energetic reserves. As such, our results are in line with the predictions of recent game-theoretical modelling on the emergence of leaders in foraging pairs. When taking into account that the qualities of individuals can differ, the resulting changes in behaviour may be complex (Rands et al. 2008). Our findings suggest that also in other social species and particularly in other cooperative breeders the determinants underlying variable leadership in movement decisions might be equally diverse.

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CHAPTER 3

Location and group size influence group decisions in simulated inter-group encounters in banded mongooses

to be submitted

Location and group size influence group decisions in simulated inter-group encounters in banded mongooses

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ABSTRACT

In social species that cooperatively defend territories the decision to retreat or attack in contests between groups is likely to depend on ecological and social factors. Previous studies have emphasized the importance of the encounter location or the size of competing groups on the outcome. In addition, the identity of the intruder, whether familiar or stranger, may also play a role. To identify the factors affecting the resident group's decisions during impending contests we simulated inter-group encounters in banded mongooses (*Mungos mungo*). When spotting rival groups banded mongooses emit 'screeching calls' which lead group members to bunch up. With playbacks of these calls, we tested how the groups' response was affected by the following factors: i) the number of resident individuals; ii) the location of the playback in relation to their territory (core versus overlap); and iii) the origin of calls (neighbor versus stranger) used. We found that subjects were more likely to approach the speakers and arrive at the speakers in the core zone than in the overlap zone. Moreover, larger groups tended to be more likely to move towards the speakers and were also more likely to arrive there. The origin of calls used in the playbacks did not affect the groups' responses. These findings exemplify the importance of the combination of location and group size concerning group decisions in impending inter-group contest. In addition, the immediate response of the smallest group to always retreat and the largest group to always attack indicates that experience of previous contests might have an influence on the decision-making process.

INTRODUCTION

Contests between territorial groups often include high costs and it is therefore beneficial for groups to assess the benefits of entering a fight or retreating depending on the ecological and social context (Wilson et al. 2001). In a number of species fatal consequences of inter-group contests have been described (e.g. various species of ants (Wilson 1971) yellow baboons (Shopland 1982), chimpanzees (Goodall 1986; Wilson and Wrangham 2003; Wilson et al. 2004; Townsend et al. 2007; Williams et al. 2008) and wolves (Mech 1994). Due to the severity of such encounters animals should only enter intergroup contest when the benefits appear to outweigh the costs (Parker 1974). The value of the contested resource may differ for each of the opponents (Austad 1983; Enquist and Leimar 1990). Thus, in situations of impending contest between groups, an efficient assessment of factors influencing the outcome of the contest and consequently an appropriate and coordinated response seem to be crucial for the survival of the group members. If territorial animals can reliably assess the value of the resource they fight for or the other contestant's fighting ability it is assumed that they will respond in a context-specific manner (Parker and Rubenstein 1981). Arguments from evolutionary game theory predict that the expected benefits may vary with location relative to the opponents' territorial boundaries and range defense should be highest towards the centre of the territory (Maynard Smith 1982). In line with these predictions, resident striped mice *(Rhambdomys pumilio)* were more likely to attack rivals in front of the nest than at territory boundaries (Schradin 2004). And in different species of birds and primates, the responses to calls of extra-group individuals decreased with increasing distance form the centre of the defenders' territory (Falls 1982; Raemaekers & Raemaekers 1984; Mitani 1985). Furthermore, in contests where groups compete as units, differences in group sizes of the opponents could be a major factor in determining the outcome (McComb 1992; McComb et al. 1994). Research from various species have shown that larger groups tend to defeat smaller ones (e.g. birds: Ligon and Ligon 1978; ants: Hölldobler 1981; carnivores: Cant et al. 2002; primates: Cheney 1987). Context-specific assessment could thus be expected during inter-group encounters to adjust the groups' behaviours in relation to the relative group size of the opponents (Sekulic 1982; McComb et al. 1994). Recently, automated radio telemetry analyses showed that in inter-group contests of capuchin monkeys *(Cebus capucinus)* the interaction location can outweigh numerical superiority with small resident groups defeating much larger groups near the centre of their home range (Crofoot et al. 2008). Hence, while analyzing

contest outcome in social species that show cooperative territorial defense it is necessary to focus on the interaction between territory location and group size.

Another case of context-specific territorial response is when territory holders differentiate between neighbors and strangers. In flat lizards *(Platysaurus broadleyi)* males respond less aggressively towards neighbors than strangers (Whiting 1999), which is described as 'dear enemy effect' (Fisher 1954; reviewed in Ydenberg et al. 1988; Temeles 1994). Alternatively the opposite phenomenon, called the 'nasty neighbor effect' (Müller and Manser 2007), has been described for some species with intense competition between neighbors. Here, individuals respond more intensely to familiar neighbors than to strangers (Godard 1993; Olendorf et al 2004; Müller and Manser 200 ├7). Thus, social living animals may only attack intruders, which represent a threat to them, because reduced aggression allows conservation of time and energy and reduces the risk of injuries (Wilson 1975).

In this study, we investigated what factors influence the group's decisions during simulated inter-group encounters in banded mongooses *(Mungos mungo)*. Banded mongooses are territorial, cooperative breeders whose home ranges often overlap with those of their neighbors (Rood 1975; Müller and Manser 2007). They mark their home range borders with faeces, urine and secretions of the anal glands which are inspected intensively when encountered by neighbors (Rood 1975; Müller and Manser 2007). Competition between social groups is intense and inter-group encounters are common and may involve withdrawal of one group but often include physical contact and severe aggression and may sometimes have fatal consequences. (Rood 1975; Cant et al. 2002; Gilchrist and Otali 2002; Müller and Manser 2007). During our study period we witnessed two incidents of individuals within the study population being involved in fatal inter-group aggression (R. Furrer and N. Jordan, personal observations). Most encounters take place when social groups come across each other in the overlap zones of their home ranges but sometimes encounters can take place deep within the home range of a group (Cant et al. 2002). Encounters are initiated when individuals detect rivals, stand erect and start producing screeching calls (Figure 1), which result in the group members bunching together (Cant et al. 2002; Furrer and Manser 2009). Consequently, individuals of the second group normally also see or hear their rivals and respond with calling and bunching up as well. In the later stages of the encounter, bunched groups might face each other closely and individuals of both groups may fan out and engage in one-to one fights or chases until one of the groups retreats (Cant et al. 2002).

We investigated whether social groups respond in a context-specific manner during impending contests between rival groups. With playbacks of screeching calls we simulated intruding mongooses that had spotted the resident group and started calling. We analysed what factors may influence the resident group's decisions at the beginning of an inter-group encounter. In particular, we investigated how the resident group's responses were affected by the location of the playback (core zone vs. overlap zone), by the number of individuals of the resident group that were present and by the origin of the call (neighbor vs. stranger) used in the playbacks. At the beginning of natural encounters between banded mongoose groups, when opponents are still distant, intruders may often be obscured by thick vegetation such as shrubs or long grass. Therefore, at that stage, acoustic cues are likely to provide more useful information about the intruders than are visual cues. However, since not all intruders call at the same time it may be difficult for individuals of the resident group to assess how many intruders may be present. Thus, we standardized the number of calls used in each playback. We predicted, according to evolutionary game theory, that the location of the playback influenced the residents group's responses. We also predicted that the number of individuals of the resident group would influence their group responses. Banded mongooses can discriminate between olfactory cues of neighbors and strangers (Müller and Manser 2007). However, as acoustic analyses showed that screeching calls do not show group-specific features (Furrer and Manser 2009) we predicted that in playbacks the origin of calls used would not have an impact on the group's responses.

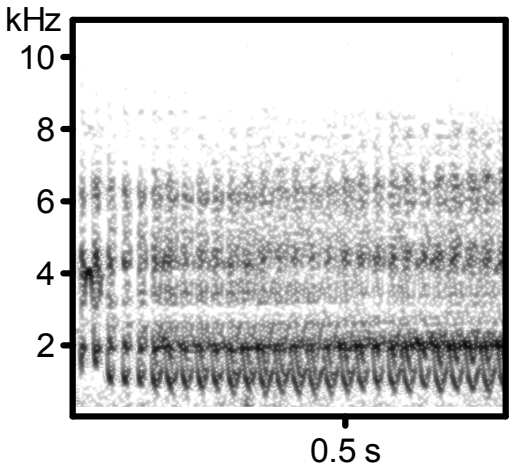


Figure 1. Spectrogram of a screeching call produced at the beginning of an inter-group encounter (FFT length: 1024, Flat Top window, overlap: 96.87%, time resolution 4.25 ms, frequency resolution: 47 Hz).

METHODS

Study site and animals

This study was conducted between October 2006 and November 2007 on a wild population of banded mongooses living on and around Mweya Peninsula, Queen Elizabeth National Park, Uganda (0°12'S; 29°54'E). The vegetation of the study site is mainly short grassland interspersed with numerous dense thickets. Details on habitat and climate are given elsewhere (Cant 2000; De Luca and Ginsberg 2001). The study population consisted of six habituated social groups allowing close-range observations and playback experiments. Additionally, we collected data on the spatial distribution of two semi-habituated groups and one wild group. Group sizes ranged from 7 to 44 individuals. Animals were classified as adults (>12 months), sub-adults (6-12 months), juveniles (3-6 months) and pups (<3 months). For individual identification, all individuals were trapped on a regular basis. Adults were fitted with color coded plastic collars. Sub-adults and infants were marked by shaving a small area of fur of the rump and pups were individually marked by coloring small areas of fur with hair-dye. All individuals were located, trapped and marked using methods that are in accordance with ASAB/ABS guidelines for the use of animals in research and are described in detail elsewhere (Cant 2000; Hodge 2007; Jordan et al. in press).

Home range estimation

We estimated the home ranges of the focal group and the adjoining groups to test whether the chosen playback locations for either the core zone or the overlap zone of the focal group were correct. To do so, we recorded location data using handheld Garmin® 12 Global Positioning System (GPS) units, and transferred into the GIS software program ArcGIS© 9 (Environmental Systems Research Institute, Redlands, California). Coordinates were taken every 15 minutes after the group had left their overnight den, continuing until the end of the observation period. We accounted for potential shifts in home range use over time, by using GPS points collected during nine month prior to the experimental day only. To maximize independence between GPS points, we extracted a single randomly selected coordinate from each observation session (Jordan et al. 2007). The selected GPS-points were plotted into ArcMap® (Environmental Systems Research Institute, Redlands, California) and the groups' home ranges were estimated using HRT tools (Hawth's analysis tools for ArcGIS) in ArcMap®. We employed the 95% fixed kernel method (Worton 1989) and used a reference bandwidth of 0.4 for smoothing. For each experiment home ranges were estimated for the

experimental group and all the adjoining groups from 146 ± 54 (mean ± SD) coordinates per social group (range: 55-249), which is sufficient for home range analysis (Seaman et al. 1999; Borger et al 2006). Groups were classified as 'neighbors' (overlap of the 95% kernel) or 'strangers' (no overlap at the 95% kernel).

Recording of screeching calls

We recorded calls that were emitted during the first stage of encounters between two groups of banded mongooses when members of the two different packs saw each other, stood erect and started calling. We quickly moved to the place where the rival banded mongooses were sighted and identified the caller. Calls were recorded within three meters of the caller using a Marantz PMD670 solid state recorder (.wav format, sampling frequency of 44.1 kHz, resolution 16 bit) and a Sennheiser ME 66/K6 directional microphone. We recorded calls from several individuals per group during 14 inter-group encounters involving each of the six habituated groups.

Playback Experiments

(a) Test stimuli

For each playback we selected screeching calls of a particular foreign group with a good signal to noise ratio. To simulate several intruders, we created two different files containing a series of calls that lasted for 30 s using AVISOFT-SASLab pro 4.38. We avoided pseudoreplication by creating two unique files for each playback. We standardized the number of calls used for each playback. This was done because firstly the members of the resident group often do not see all intruders as vision can be blocked by vegetation. Secondly not all intruders usually call at the same time. Therefore, for members of the resident group, it may often be difficult to assess how many intruders are present. The amplitude of the calls used in the playbacks was adjusted to the observed amplitude of calls (max. 80 dB) when subjects encountered foreign mongooses, and was measured with a digital sound level meter SL-100 (Voltcraft; sound level range: 30 to 130 dB, frequency range: 31.5 Hz to 8 kHz, response time: 100-125 milliseconds, resolution 0.1 dB).

(b) Experimental design

Prior to playback experiments we followed the focal group of banded mongooses on foot for at least thirty minutes and recorded the presence of individual group members. We only performed playbacks if the focal group had not encountered rival conspecifics or predators

during the observation period. We then placed two loudspeakers (JBL on Tour; frequency range: 100 Hz-20 kHz, power consumption: 6 W maximum) on the ground along the predicted foraging route with a distance of two meters between them. The loudspeakers were covered by vegetation, and each of them was connected with a Marantz PMD670. We then selected a location where we intended to gather the focal group prior to the playback as 'start location'. This spot was situated in an open area at a previously measured distance 25 meters from the speaker. When the focal group came close we attracted the individuals to the start location by distributing a small quantity of bait (approximately 20 g of a mix of rice and gravy) on the ground within a circle area of 1m diameter. As soon as individuals finished searching for bait and began to move away again the playback was started. To collect data on the subjects' responses one person recorded their behavior at the start location using a camcorder (Sony mini DV Digital Video Camera, model DCR - HC37E) while another person watched at a distance of five meters from the speakers, to make detailed observations of the area close to the speaker. Focal groups always responded by bunching up and then subjects started moving as a close unit. We recorded the following group responses to playbacks: a) the first movement direction of the focal group as an immediate response b) whether they arrived at the speakers as an final response; and c) if the focal group arrived there we measured the time until the first subject arrived within a distance of one meter to the speakers using a stop-watch (M-Quartz alarm chronograph, Switzerland). To avoid habituation, only one playback was conducted per group per day followed by a period of at least seven days without the same or a similar type of playback. We performed the playbacks either in an area of exclusive use of the focal group (core zone: where we had not recorded foreign mongooses during the 9 month period prior to the experiment; however, foreign mongooses may still occasionally have entered this core zone; Figure 2a) or in a border area shared with one or several adjoining groups (overlap zone; Figure 2b). We counted the number of group members present during the playbacks (adults, non-adults). This number could vary slightly within the social groups because some individuals may have died or disappeared or dependent pups became infants in the time between the playbacks. As stimuli we used screeching calls either recorded from a neighbor or a stranger group. In each group we conducted one playback in the core/overlap zone using calls recorded from neighbor/stranger mongooses.

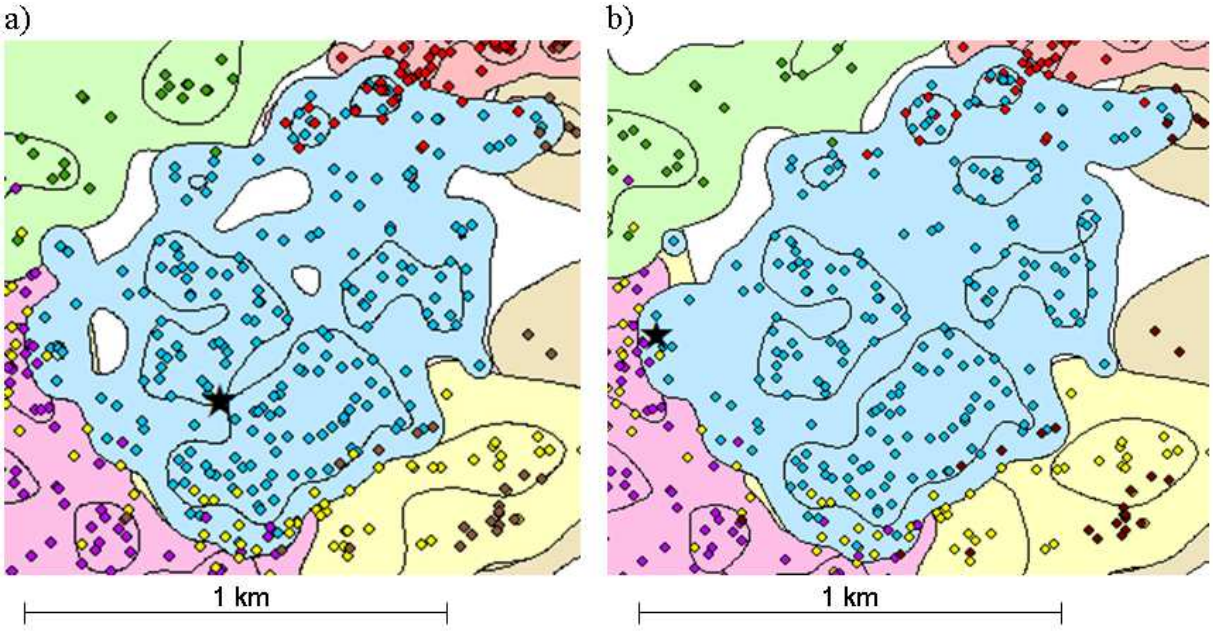


Figure 2. Sample home ranges maps of a focal group (light blue) and the adjoining social groups are shown. Each home range is confined by the 95% fixed kernel line and core areas for each home range are confined by the 50% fixed kernel line. Each dot represents a group's location that was randomly selected from all the GPS locations collected during an observation session. GPS-points collected during a period of 9-months prior to the playback were incorporated in the maps. The stars represent the locations of playbacks which were conducted either in an area used exclusively by the focal group (core zone; figure 2a) or in an area shared with adjoining groups (overlap zone; figure 2b).

Statistical analyses

Statistical tests were performed using R 2.8.1 (R Development Core Team 2008). To analyse the factors that might affect the group's immediate and final responses to playback of screeching calls we conducted generalized linear mixed-effect models (GLMMs; see Crawley 2002, Bolker 2009) with binary response variables, binomial error structure and logit-link function. We controlled for the repeated sampling of the same group with 'group' fitted as a random factor (Crawley 2002) using the package lme4 (Bates et al. 2008). We first constructed full models, including the three fixed factors (playback location, all group members or adult group members, calls origin) and tested the overall significance of the full model against the null model including the intercept and the random factor only (Johnson and Omland 2004). We then used the corrected Akaike's Information Criterion (AICc: Hurvich and Tsai 1989) to select the most parsimonious model with the best fit to the data (Johnson and Omland 2004). This approach avoids problems of repeated significance testing (Mundry and Nunn 2009). We used likelihood ratio tests to test the overall significance of each model compared to the null model and the significance of each individual factor compared to a

reduced model without the factor of interest. Since the likelihood ratio (LR) tested against a Chi-square approximation tend to overestimate effect size (Bolker et al. 2009) we used parametric bootstrapping with 1000 Monte Carlo simulations to generate a distribution of LR from the fitted parameter estimates and tested the observed LR against this distribution (Faraway 2006). For the Monte Carlo simulations we used the packages arm (Gelman et al. 2007) and faraway (Faraway 2005).

Furthermore, in playbacks where subjects arrived at the speakers we analysed whether the group size of the focal group influenced on the time to approach the speakers. After counting the number of individuals present in each playback experiment we calculated a mean group size and assigned each group a rank according to group size. We conducted a Spearman rank correlation to test whether the time to approach the speakers correlated with the groups' ranks. We also performed Spearman rank correlations to investigate whether the number of individuals of all age categories and the number of adult individuals present in each experiment correlated with the time to approach the speakers.

RESULTS

Immediate response to playbacks

Focal groups responded to all playbacks of screeching calls. At first, subjects responded by producing worry calls (Figure S1; see Müller and Manser 2007) and looking towards the speakers while standing on their hind legs. Then subjects bunched up and often produced screeching calls themselves and sometimes scent marked other mongooses and marked the ground. Afterwards, all subjects either moved towards the speakers or away from them as a cohesive group and often produced moving calls (Figure S2). For the analyses we used the full model as the exclusion of any of the parameters did not improve the model fit by 2 AICc units. The full model for the immediate response explained significantly more variance in the data than the null model (LR = 18, df = 3, $P = 0.006$). The first movement direction of the subjects was influenced by the location of the playback. Focal groups were more likely to approach the speakers in the core zone than in the overlap zone (LR = 11; df = 1, $P = 0.016$; see Table 1 for the values of the factors in the full model). The subjects' first movement direction was also influenced by the number of group members of the resident group. Larger groups tended to be more likely to move towards the speakers than small ones (LR = 7.07; df

= 1, P = 0.073; Figure 3a). Whether the calls used in the playbacks were recorded from a neighbor or a stranger group did not influence the resident groups' first movement direction (LR = 0.22; df = 1, P = 0.55). We then replaced in the full model the number of group members with the number of adult individuals present. Here, groups with more adult individuals were significantly more likely to move towards the speakers as an immediate response than groups with fewer adult individuals (full model against null model (LR = 21, df = 3, P = 0.003; number of adult individuals present (LR = 10; df = 1, P = 0.024; Table 1b, Figure 3b). The LR and the P-values of the factors playback location and calls origin remained very similar to the ones of the full model including all group members.

Final response to playbacks

The focal groups' final responses were influenced by the playback location and group size of the focal groups, but not by the origin of the calls. For the analyses we used a reduced model as the exclusion of 'calls origin' improved the model fit by 2 AICc units. The reduced model for the final response explained significantly more variance in the data than the null model (LR = 16.1, df = 2, P = 0.007). Subjects were more likely to approach to within 1m of the speakers in the core zone of their territory than in the overlap zone (LR = 11.4; df = 1, P = 0.001, see Table 2 for the values of the factors in the reduced model) and larger groups were more likely to arrive at the speakers than were smaller groups (all groups members; LR = 5.11; df = 1, P = 0.022; Figure 3c). When replacing the number of group members with the number of adults present, groups with more adult individuals were also more likely to arrive at the speakers than groups with fewer adults (reduced model against null model (LR = 17.5, df = 2, P = 0.001); number of adult individuals present: (LR = 6.5; df = 1, P = 0.025; Table 2b; Figure 3d). The LR and the P-values of the factors playback location and call origin remained very similar to the ones of the reduced model including all group members.

Tables 1 and **2**. Factors influencing the focal group's immediate and final responses to simulated intrusion playbacks. Shown are the values for all group members (a) and adult individuals only (b) for the predictor variables (playback location; group size; call origin) used in the GLMMs.

Predictor variable	β (estimate) ± SE	z	*P*-value
1. Immediate response			
Intercept a)	-1.14 ± 3.88	-0.29	0.77
b)	0.09 ± 5	0.018	0.98
Playback location a)	4.3 ± 1.8	2.39	0.017
b)	4.04 ± 1.64	2.46	0.014
Group size a)	-0.28 ± 0.14	-1.96	0.049
b)	-0.5 ± 0.3	-1.68	0.093
Call origin a)	0.61 ± 1.78	0.46	0.65
b)	0.76 ± 1.66	0.34	0.731
2. Final response			
Intercept a)	0.116 ± 4.670	0.025	0.980
b)	-0.140 ± 4.106	-0.034	0.973
Playback location a)	5.481 ± 2.176	2.519	0.012
b)	4.532 ± 1.736	2.610	0.009
Group size a)	-0.377 ± 0.213	-1.771	0.077
b)	-0.480 ± 0.297	-1.618	0.106

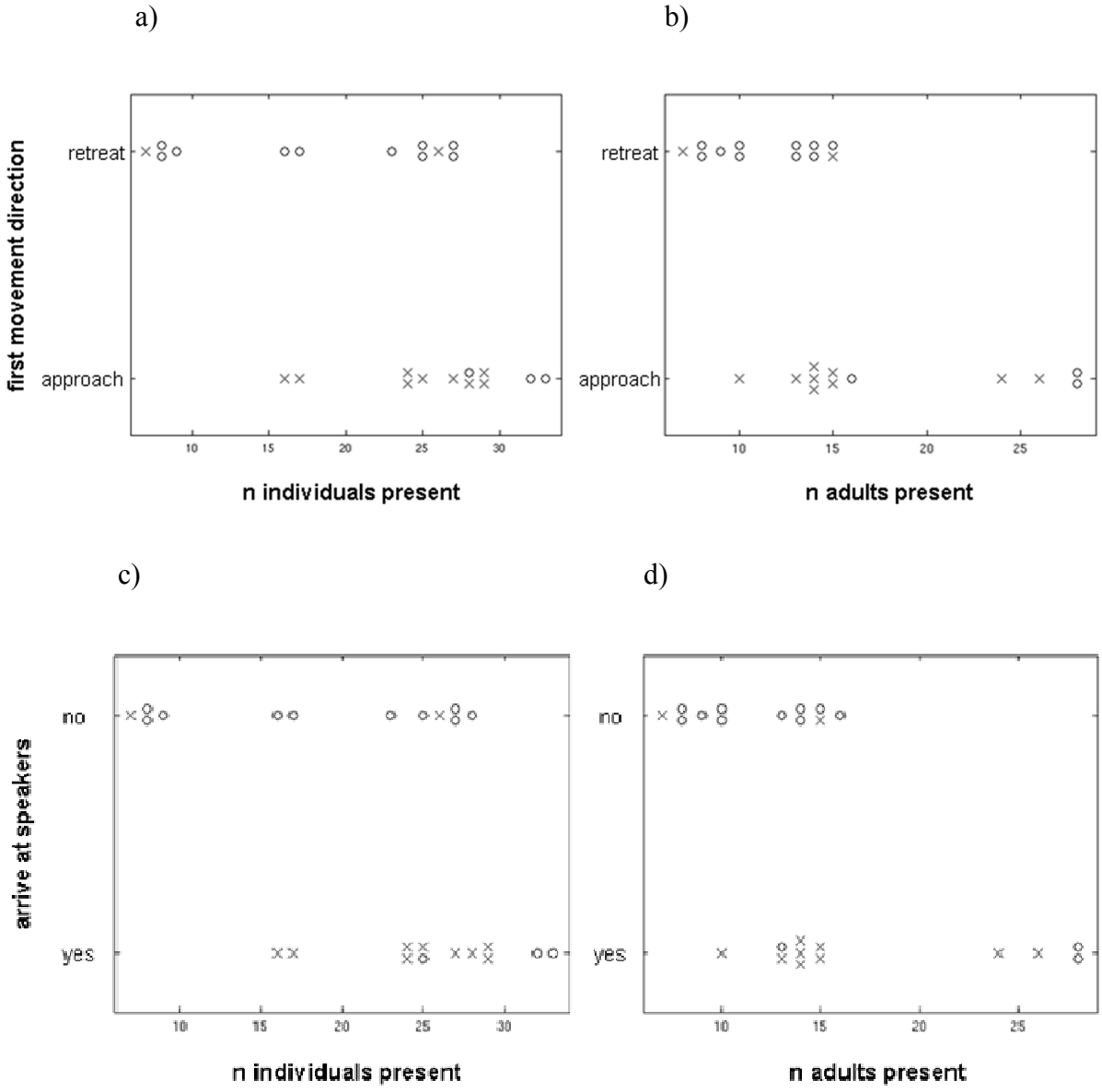
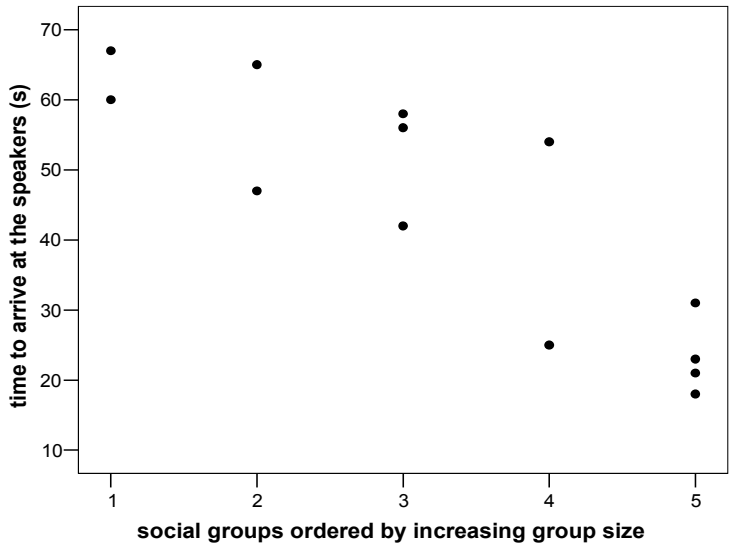


Figure 3. The effect of the total number of individuals and the number of adult individuals present during the playbacks on the likelihood to approach the speakers as an immediate response (a), (b) or to arrive at the speakers as an final response (c), (d). (o) represent playbacks conducted in the overlap zone, (x) represent playbacks carried out in the core zone.

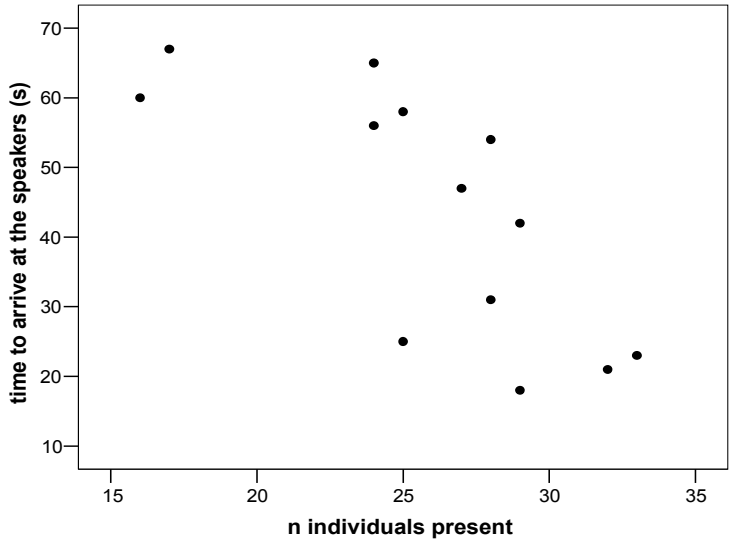
Time to arrive at the speakers

Group size was negatively correlated with the time to arrive at the speakers, with large groups arriving there faster than small ones (Spearman rank correlation; r_s = -0.878, N = 13, P < 0.001; Figure 4a). The number of individuals of all age categories and the number of adult individuals present during the playbacks were negatively correlated with the time to arrive at the speakers (Spearman rank correlation; all age categories; r_s = -0.848, N = 13, P < 0.001; Figure 4b); adult individuals; r_s = -0.813, N = 13, P = 0.001; Figure 4c).

a)



b)



c)

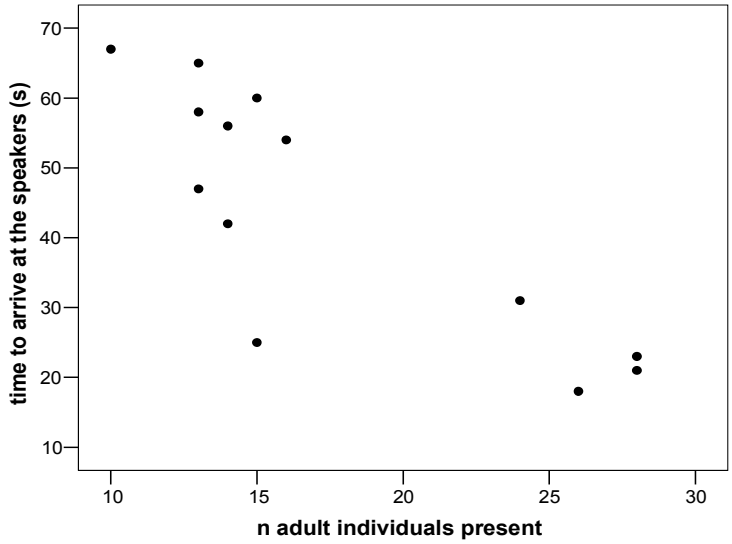


Figure 4. Scatter plots showing: a) the effect of social groups ordered by increasing group sizes b) the influence of the number of the individuals present during the playbacks c) the effect of the number of adult individuals present on the time to arrive at the speakers (s). Note that the smallest study group is not included in the graph as it never arrived at the speakers.

DISCUSSION

Banded mongoose group decisions in simulated inter-group encounters depended on the experiment location and the number of resident individuals (in particular, the number of adult individuals) present, but not on the origin of calls played back to them. Resident groups reacted in situations of impending contest in a context-specific manner with the location of the playback influencing the first movement direction and the likelihood to arrive at the speakers. Subjects were more willing to move towards and arrive at the speakers in the core zone of their territory than in an overlap zone used by two or several groups. These results are in line with predictions from evolutionary game theory suggesting that the expected benefits of participation in inter-group conflicts may vary with the location relative to the opponents' territorial boundaries, and predicting that range defense should be highest towards the centre of the territory (Maynard Smith 1982). Furthermore, the conflict hypothesis (Tinbergen 1952; Hinde 1970) explains the variation in territorial defense of single individuals as a result of the interaction between aggression and fear which, according to this hypothesis, are opposing motivational states. When aggressive tendencies exceed fearful tendencies, as happens in the territory center, an individual is likely to attack (Archer 1988). This interaction between

aggression and fear may equally influence the group's decision in an impending inter-group encounter. Experiments with single individuals showed that male sticklebacks *(Gasterosteus aculeatus)* attack neighbors more intensely inside their territory than outside (Bolyard and Rowland 2000) and striped mice chase away intruders inside their own territory but not at the territory boundaries (Schradin 2004). In group living species, little is known about the influence of encounter location on the group's behavioral responses. In gibbons *(Hylobates lar)*, responses to calls of extra-group individuals decrease with increasing distance from the centre of the defenders' territory (Raemaekers and Raemaekers 1984). Moreover, in capuchin monkeys *(Cebus capucinus)* small resident groups appear capable of defeating much larger groups near the centre of their home range (Crofoot et al. 2008). In banded mongooses, where competition between social groups is intense and inter-group encounters are common, context-specific decisions are essential to avoid unnecessary costs. In areas of overlapping home ranges, the tested groups retreated frequently and thus avoided the potentially severe consequences of a contest. In the core zone of their territory however, groups almost always advanced and arrived at the location of the loud speakers. Thus, it seems that for banded mongooses the value of the resource (Parker 1974, Maynard Smith 1982) 'core zone', where the resident group has more or less exclusive access to its resources, is higher than the value of overlapping areas.

The direction of first movement in response to playbacks tended to be influenced by the total number of individuals of the resident group whereas this immediate response was significantly influenced by the number of adult individuals present. Both the total number of group members and the number of adult individuals had an effect on the likelihood to arrive at the speakers. The resident group's decisions were therefore influenced by the number of defenders, with larger groups being more likely to approach and to risk a contest. It was suggested that numerical assessment is widespread among species with inter-group contest (Wilson et al. 2001). Assessment of the opponent's strength in numbers was experimentally shown in lions *(Panthera leo),* where females are more willing to enter contests in which their side has a numerical advantage. For example they were more likely to approach a single roar than a chorus of three strangers' roars (McComb et al. 1994). Assessment of the number of intruders was also shown in green woodhoopoes *(Phoeniculus purpureus)*, where members of the resident group vocalized longer in response to intrusions by larger groups (Radford 2003). As all group members cackle loudly during their vocal rallies an accurate assessment of the opponent strength is possible. In banded mongooses, however, not all intruders call at the

same time after having spotted the rivals. Hence, numerical assessment of the intruder's group size at the beginning of an inter-group encounter seems unlikely. As fights between groups of banded mongooses are normally decided by group size with larger groups defeating smaller ones (Cant et al. 2002) it might be that the group's decisions at the beginning of an inter-group encounter is influenced by experience of previous fights and not on relative assessment of the opponents' strength. Studies have shown that where fish lose a fight they tend to lose again (Chase et al. 1994; Hsu and Wolf 1999). In threespine sticklebacks *(Gasterosteus aculeatus)* territorial aggression is modified by the individual's past fighting experience (Bolyard and Rowland 2000). In our study, independent of the playback location, the smallest group always retreated whereas the largest group always advanced. The willingness of the largest group to approach the speakers and arrive there to risk a contest is likely to be supported by their better body condition compared to the five other tested groups. This group had access to garbage dumps in their territory and adults of this refuse-feeding group were heavier than non-refuse feeding adults (Otali and Gilchrist 2004; R. Furrer personal observation). Numerical advantage and their higher body mass could have contributed to them winning most contests. Thus, it appears that experiences of previous encounters influenced their decisions to always approach and arrive at the speakers. In the playbacks where the focal group arrived at the speakers the time to arrive there was negatively correlated with increasing group size of resident groups, the number of individuals and the number of adults present. Larger groups arrived faster to face the simulated intruders. Because of the previous experience of larger groups in normally defeating smaller ones they appear not only to be more likely to confront the opponents but they also seem to be ready to confront their rivals more quickly.

The call origin did not have an effect on the focal group's immediate and final responses. Whether the calls used in the playbacks were recorded from individuals from a neighbor or a stranger group did not influence the focal group's first movement direction and the likelihood to arrive at the speakers. In some species territory holders differentiate between familiar neighbors and strangers (Temeles 1994). Banded mongooses discriminate between the scent marks of neighbors and strangers (Müller and Manser 2007). This ability seems to be adaptive because neighbors pose a considerable threat as potential usurpers of territories and competitors of mates (Cant et al. 2002), whereas, in contrast, strangers commonly represent small, single-sex dispersing splinters that are normally outnumbered by their same-sex individuals of the resident group and thus pose little threat (Cant et al. 2001; Müller and Manser 2007). However, in contrast to their response to olfactory cues, focal groups did not

respond differently to the screeching calls of neighbors versus the screeching calls of strangers. As screeching calls do not show group-specific features (Furrer and Manser 2009) it seems likely that banded mongooses cannot recognize calls of particular rival groups. Thus, at the beginning of an inter-group encounter, resident groups do not seem to gather information about the identity of the intruders using acoustic cues. Instead, the location and the number of defenders seem to have more influence on the group's decisions at the beginning of an inter-group encounter.

In banded mongooses, encounters between groups are normally decided by group size with the larger group defeating the smaller one (Cant et al. 2002). However, the decisions of the resident group at the beginning of an impending inter-group encounter were not only influenced by their group size. While the largest and the smallest group always responded with advancing and retreating respectively, suggesting experience of previous contests might play a role, the four medium sized groups responded context-specifically. They almost always advanced in the core zone and retreated in the overlap zone of their territory. Thus, we conclude that a combination of encounter location and the group size of the resident group influence the decisions to retreat or to approach and attack the intruders. These results are in line with predictions of evolutionary game theory suggesting that the expected benefits may vary with the location relative to the opponents' territorial boundaries. Our results suggest that in banded mongooses decisions in impending contests are made context-specifically and that experience of previous encounters might play an important role in the decision-making process. As such, our findings are likely to be of importance for other social species that show cooperative territorial defense.

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SUPPLEMENTARY MATERIAL

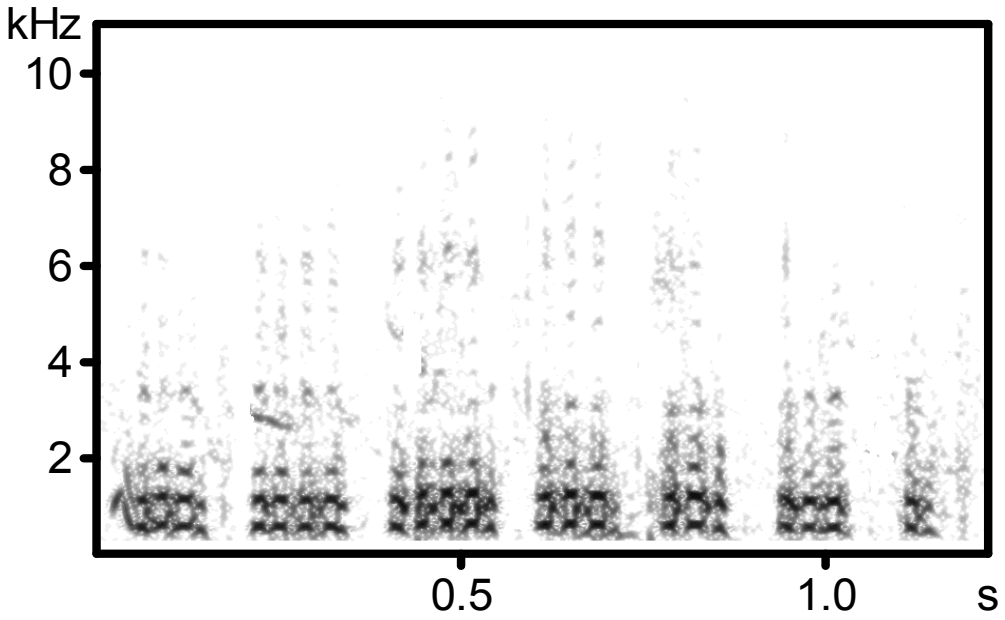

Figure S1. Spectrogram of worry calls produced at the beginning of a playback when group members faced the speakers while standing on their hind legs (FFT length: 1024, Flat Top window, overlap: 96.87%, time resolution 4.25 ms, frequency resolution: 47 Hz).

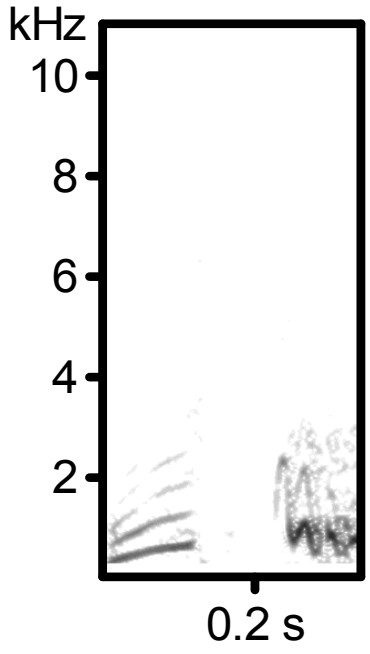

Figure S2. Spectrogram of a moving call typically consisting of two elements produced during a playback when group members approached the speakers or retreated as a group (Spectrogram parameters as above).

CHAPTER 4

Banded mongoose recruitment calls convey information about risk and not stimulus type

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Banded mongoose recruitment calls convey information about risk and not stimulus type

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ABSTRACT

Many species use specific vocalizations that attract conspecifics to food sources or that recruit other group members to inspect secondary predator cues or to mob predators. However, little is known regarding the variation in the acoustic structure of such calls and the associated meaning. In the cooperatively breeding banded mongoose (*Mungos mungo*), we investigated calls emitted in the context of group recruitment to three different stimulus types: (1) secondary predator cues; (2) snakes; and (3) members of rival groups. Calls produced in response to predator faeces differed from the harsher variants elicited by snakes and rival groups, but the latter two elicited similar calls. Only a few calls of intermediate acoustic structure were emitted in response to the different stimulus categories. Playbacks of calls elicited by the different stimuli caused individuals to approach the speaker in the same way. However, calls elicited specifically by snakes and rival mongooses resulted in a higher proportion of receivers responding and a faster receiver response than calls elicited by faeces. This suggests a graded rather than a discrete recruitment call system. Thus, despite obvious differences in stimulus type and the purpose of recruitment, the acoustic structure of calls conveys information about the risk of the encountered stimulus and not the stimulus type itself, allowing receivers to adjust their response according to the urgency. Since calling continued for prolonged periods after all group members had gathered around the callers, these calls may also function to deter rivals and to coordinate the subsequent group response.

INTRODUCTION

Birds and mammals use specific calls that attract conspecifics to approach the location of the caller (Hauser 1996). These calls lead conspecifics to food sources, which may facilitate access to them (Marzluff & Heinrich 1991), increase the signaller's chances of attracting a potential mate (Collias & Joos 1953; Stokes 1971; Marler et al. 1986a; Marler et al. 1986b), or reduce predation risk (Elgar 1986). In altricial pied babblers (*Turdoides bicolor*), breeders and helpers attract nutritionally independent but inexperienced young foragers to good feeding sites by giving 'recruitment calls' (Radford & Ridley 2006). Moreover, specific recruitment calls are also produced when social animals face potentially dangerous situations. Cooperatively breeding meerkats (*Suricata suricatta*), emit such calls when encountering secondary predator cues or snakes, and receivers respond by joining the caller either to inspect the cue or to mob the snake (Manser 2001; Manser et al. 2001). Furthermore, recent studies on vocalisations in the context of recruiting behaviour showed that mobbing calls in black-capped chickadees (*Poecile atricapilla*) vary depending on the size of the predator (Templeton et al. 2005) while in reed warblers (*Acrocephalus scirpaceus*) such calls vary systematically with the distance to the threat (Welbergen & Davies 2008). Although the recruitment function of calls produced in these different contexts has been tested experimentally (Evans & Evans 1999; Manser et al. 2001; Di Bitetti 2003; Gros-Louis 2004; Templeton & Greene 2005; Radford & Ridley 2006; Welbergen & Davies 2008), little is known about how differences in the context of production affect the calls' acoustic structure.

The acoustic structure of alarm calls inducing vigilance or flight responses often varies with the context in which these calls are produced (Marler 1955; Sherman 1977). Alarm calls may encode information about the level of urgency to respond (Robinson 1981; Blumstein & Armitage 1997; Leavesley & Magrath 2005), denote the class of predators (Seyfarth et al. 1980; Gyger et al. 1987) or both (Manser 2001). Alarm calls signalling urgency appear to contain information about the risk the caller is facing (Robinson 1981) in a similar way as described for mobbing calls. On the other hand, functionally referential alarm calls denote the approaching predator type and contain information about specific objects or events in the external environment (reviewed in Macedonia & Evans 1993; Searcy & Nowicki 2005). The evolution of calls that are specific to predator type has been shown to relate to (1) differences in escape behaviours (Macedonia & Evans 1993), even if these are small (Manser 2001, Furrer & Manser 2009), or (2) an ability to locate the predator more quickly (Kirchhof &

Hammerschmidt 2006). In line with these results, the analysis of the structural variation of recruitment calls may reveal graded differences according to the level of urgency or categorical differences in acoustic structure depending on stimulus type.

We investigated recruitment calls in banded mongooses (*Mungos mungo*), a small (less than 2 kg), cooperatively breeding diurnal herpestid living in mixed-sex groups of 5-44 individuals (Cant 2000). They are preyed on by mammalian predators, reptiles such as the African rock python *(Python sabae)* and large raptors such as martial eagles (*Polemaetus bellicosus)*, which were seen to target them at the study site (Rood 1983; Otali & Gilchrist 2004; Bell 2006). For banded mongooses group life provides individual protection, as group members gather to inspect secondary predator cues (Müller & Manser 2007) and bunch together to attack predators and competitors (Rood 1975). When inspecting secondary cues, such as faeces or urine of predators, individuals emit shrill calls that seem to recruit other group members (R. Furrer, personal observation). Similarly sounding vocalizations are produced while mobbing reptiles, chasing mammalian predators, such as rusty-spotted genets (*Genetta maculata)* (Banded Mongoose Project, unpublished data), and attacking raptors (Rood 1983). Rival banded mongooses from foreign social groups are fiercely attacked during inter-group interactions, which can be fatal (Rood 1975; Cant et al. 2002; Gilchrist & Otali 2002). At least two adult individuals of the study population died in agonistic interactions during the period of this study (Banded Mongoose Project, unpublished data). During such encounters individuals produce 'screeching calls' (Cant et al. 2002) also named 'war cries' (Müller & Manser 2007), and these calls seem to alert the rest of the group, recruiting individuals of each group to bunch together and approach the other group *en masse* (for details on inter-group encounters see Cant et al. 2002).

We examined the acoustic structure of calls produced during encounters with different stimulus types that recruited other group members. In particular we investigated the vocalizations given when: (1) inspecting predator faeces; (2) mobbing African rock pythons; and (3) facing rival groups. We then systematically tested whether the information content of calls emitted in each context was meaningful to recipients with playback experiments. We expected little overlap of call structure between the different stimulus types and appropriate, potentially different response strategies if calls were functionally referential. Alternatively, if the calls relate to the urgency to respond we expected their acoustic structure to grade along a continuum according to the risk of the context and predicted only urgency-based differences

within a single response strategy. Thereby, we assumed that predator faeces posed a lower risk to banded mongooses than snakes or rival mongooses. Although it is more difficult to give an a priori assumption about the risks snakes and rival banded mongooses pose, it is likely that, once detected, snakes might pose a slightly lower immediate risk for the caller than rival mongooses. This is because the caller could easily avoid a detected snake by moving away, whereas this is less possible for a caller attacked by rival mongooses.

METHODS

Study site and animals

Data were collected from July to December 2006 and from May to December 2007 on a wild population of banded mongooses living on and around Mweya Peninsula, Queen Elizabeth National Park, Uganda (0°12'S; 29°54'E; for details of the study area see Cant 1998; Gilchrist 2001). The study population consisted of six groups of habituated banded mongooses totalling 150 adult individuals that allowed close-range observations. Animals were classified as adults (>12 months), sub-adults (6-12 months), juveniles (3-6 months) and pups (<3 months). For individual identification, adults were fitted with color coded plastic collars. Sub-adults and infants were marked by shaving a small area of fur on the rump, and pups by dyeing small areas of fur with blonde hair-dye (see Cant 2000 for descriptions of trapping and marking techniques). Trapping and experiments were conducted in accordance with ASAB/ABS guidelines for the use of animals in research and all procedures were approved by the Uganda Wildlife Authority and Uganda National Council of Science and Technology.

Recording methods

To determine whether the acoustic structure of calls varies between different contexts, we focused on calls elicited by predator faeces, African rock pythons and rival conspecifics. Calls were recorded within 3 m of the caller using a Marantz PMD670 solid state recorder (.wav format, sampling frequency of 44.1 kHz, resolution 16 bit) and a Sennheiser ME 66/K6 directional microphone. We recorded calls produced in response to secondary predator cues by putting fresh faeces deposited by the predator during the previous night on the predicted foraging route. As stimuli we used faeces deposited by leopards *(Panthera pardus)*, and lions *(Panthera leo)*, which are both common predators at the study site. We conducted 15 presentations with lion faeces and 12 with leopard faeces in six groups. The two predator

species may represent different threat levels to banded mongooses as leopards are known to prey on mongooses (Hayward et al. 2006), whereas banded mongooses do not appear on the lion's prey species list (Hayward & Kerley 2005). Faeces from adult lions exceed 35 mm in diameter and were therefore clearly identifiable (Bodendorfer et al. 2006). Since faeces deposited by leopards could be confused with faeces of immature lions we were advised on species identification by specialists of the Uganda Large Predator Program. We recorded calls emitted in response to natural encounters with African rock pythons and rival banded mongooses. In both cases we quickly moved to the place where either the snake was confronted or the rival banded mongooses were sighted and recorded the calls. In the latter case we recorded calls that were emitted during the first stage of encounters between two groups of banded mongooses when members of the two different packs sighted each other, stood erect and started calling. After group members bunched up to confront the snake or the rival banded mongooses we stopped recording calls as they often overlapped and could not be assigned to a particular individual. Because calls elicited by African rock pythons and rival mongooses were recorded during natural encounters, there was a delay in recording of 5-15 seconds after the first call had been given. We recorded calls emitted during seven encounters with African rock pythons in five groups and calls elicited by conspecifics from 14 inter-group encounters involving each of the six groups. We used calls from one or several callers per presentation or encounter and analysed the first call produced by an adult individual that had good signal to noise ratio.

Acoustic analyses

To generate spectrograms of calls we carried out 1024-point fast Fourier transformation (Hamming window; overlap: 93.75%; time resolution 1.45 ms; frequency resolution: 43 Hz) of all calls using AVISOFT-SASLab pro 4.38 (R. Specht, Berlin, Germany). We measured 18 acoustic parameters from the spectrograms (see Table 1 for parameters used in the different analyses). Including many acoustic parameters enables an analysis of complex patterns without a priori assumptions of the importance of specific parameters (Schrader & Hammerschmidt 1997). Analyses included parameters describing temporal and frequency dynamics and entropy of calls. For frequency- and entropy-related parameters we chose the mean spectrum of the entire element and the centre of the element as temporal locations of the measurements.

Table 1. Acoustic parameters used in the discriminant function analyses. Acoustic parameters used in the DFA's of calls elicited by lion and leopard faeces respectively (1) and parameters used to test classification probabilities comparing calls produced in response to predator faeces, African rock python and rival mongooses (2). All correlation parameters with $r_s > 0.8$ were excluded from the parameter set. Either the location of the measurement of the acoustic parameter was in the centre of the call (centre) or a mean value of the acoustic parameter was calculated over the whole call (mean).

acoustic parameter	parameter category	analysis
entropy (centre)	entropy	1
entropy (mean)	entropy	1, 2
frequency bandwidth (mean)	frequency distribution	1, 2
maximum frequency (centre)	frequency	1
maximum frequency (mean)	frequency	1
maximum frequency of quartile 25 (mean)	frequency distribution	2
maximum frequency of quartile 50 (mean)	frequency distribution	1
maximum frequency of quartile 75 (centre)	frequency distribution	1
number of peaks (mean)	frequency distribution	2
peak frequency (mean)	frequency	2

Playback experiments

(a) Selection and amplitude of calls

To test whether receivers extract specific information from calls produced in different contexts, we carried out playback experiments. We selected calls with the typical acoustic structure of the context and a good signal to noise ratio. We avoided pseudoreplication by creating for each playback a unique file lasting 30 s. To test specifically the influence of the acoustic structure, we standardized the number of calls used in all playbacks. Each file contained 12 calls emitted by two to four individuals of the same group during the same event. The amplitude of the calls used in the playbacks was adjusted to the observed amplitude of calls when subjects encountered the stimuli and was measured with a digital sound level meter Voltcraft SL-100 (sound level range: 30-130 dB; frequency range: 31.5 Hz-8 kHz; response time: 125-1000 ms, resolution 0.1 dB) (Conrad Electronic, Hirschau, Germany).

(b) Experimental design

Calls used in playbacks were elicited by leopard and lion faeces, African rock pythons and rival banded mongooses. We conducted 43 playbacks in six groups in a randomized order. Prior to the playback experiments, we verified the presence of all individuals of the focal group. We then placed the loudspeaker (JBL on Tour (Harman Multimedia, Northridge,

U.S.A.); frequency range: 100 Hz-20 kHz; power consumption: 6 W maximum) on the ground along the predicted foraging route, so that it was covered by vegetation, and connected it to a Marantz PMD670. Afterwards we defined a location where we intended to gather the focal group prior to the playback as the 'start location'. This spot was situated in an open area at a previously measured distance 20 m from the speaker. When the focal group came close we attracted the individuals to the start location by distributing a small quantity of bait (approximately 20 g of a mix of rice and gravy) on the ground within a circle of 1m diametre. As soon as individuals finished searching for bait and began to move away again, the playback was started. To collect data on the subjects' responses one person observed their behaviour at the start location while another watched from a distance of 5 m from the speaker, to make detailed observation of the area close to the speaker. We observed the subjects' responses to playback, measured the time until the first subject arrived within 1 m of the speaker using a stop-watch (M-Quartz alarm chronograph; Mondaine Watch Ltd, Zurich, Switzerland) and counted out of the total number of group members present the number of subjects arriving within 1 m of the speaker. As a control treatment, we recorded calls of the yellow-fronted tinkerbird *(Pogoniulus chrysoconus),* and conducted six control playbacks with the same design. Yellow-fronted tinkerbird calls were chosen as control stimuli because these non-threatening conspicuous calls are produced over prolonged periods. We only performed playbacks if the focal group had not encountered predator faeces, snakes or rival conspecifics during the previous 30 min. To avoid habituation, only one playback was conducted per group per day followed by a period of at least 7 days without the same or a similar type of playback.

Statistical analyses

(a) Acoustic analyses

Statistical analyses were conducted using SPSS 13.0. (SPSS Inc., Chicago, Il, U.S.A.). To exclude acoustic parameters that correlated highly with others we conducted Spearman correlations (exclusion criteria: $r_s > 0.8$). The remaining parameters were entered into a discriminant function analysis (DFA) to determine classification probabilities of calls produced. DFA identifies linear combinations of predictor variables that best characterize the differences between groups and assigns each call to its appropriate group (correct assignment) or to another group (incorrect assignment). For external validation, we used a leave-one-out cross-validation procedure and to test the significance of the classification level achieved, two-tailed binomial tests were performed. To fulfil the requirements of independence in DFA

(Mundry & Sommer 2007) parameters of only one randomly chosen call per individual were entered into the DFA. For each stimulus category, calls recorded from individuals of both sexes and from all groups available, were entered into the DFA. As the entered number of calls from each sex and group was not fully balanced overall, we conducted post-hoc DFAs to control for possible sex- or group-specific call characteristics.

(b) Playback experiments

Statistical tests were performed using R 2.4.1 (R Development Core Team 2006). To analyse the influence of the stimuli eliciting the calls used in the playbacks on the time to approach the speaker and the percentage (%) of group members approaching, we carried out linear mixed-effect models (LMMs). In these analyses we controlled for the repeated sampling in the same group with 'group' fitted as a random factor (Crawley 2002) by conducting random intercepts models using the packages nlme (Pinheiro et al. 2006) and MASS (Venables & Ripley 2002). Since the order of playbacks was randomized in each group and the identity of the first individual approaching the speaker varied greatly, we omitted these factors from the statistical models. To fulfil the requirements of normally distributed data we used logarithmic and arcsine-transformed data (Sokal & Rohlf 1995).

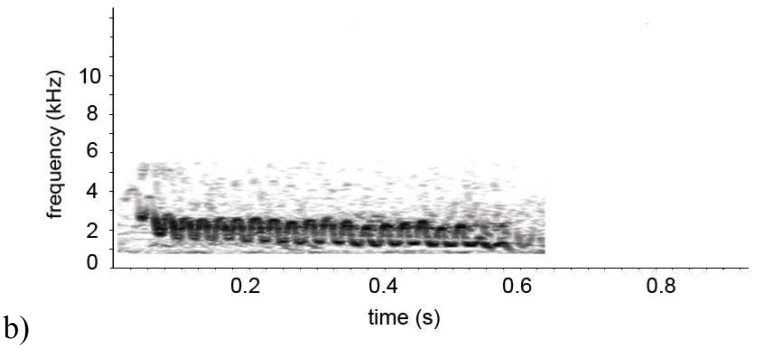
RESULTS

Acoustic structure of recruitment calls

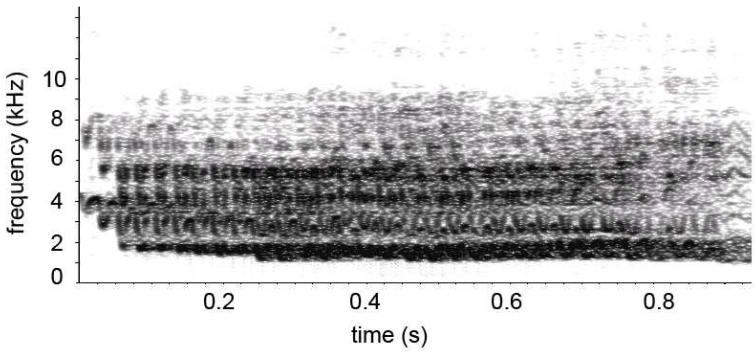
The three different stimuli elicited calls with two acoustically distinct structures which graded into each other. Individuals produced calls with a comparatively small frequency bandwidth when detecting predator faeces (Figure 1a) and calls with large frequency bandwidth when encountering snakes or rival banded mongooses (Figure 1b). Calls showing intermediate characteristics were elicited by all stimuli (Figure 1c). The classification probabilities of calls elicited by leopard faeces (N = 16) versus lion faeces (N = 16) showed that the first discriminant function explained 100 % of the total variance. The first function of the DFA showed 56.3 % correct cross-validated assignment to the appropriate context (Wilk's Lambda = 0.79, χ^{2} = 6.25, df = 7, P = 0.51) a level not substantially higher than expected by chance (50 %) (binomial tests: leopard faeces: N = 16, P = 0.8; lion faeces: N = 16, P = 0.8). We therefore randomly selected nine calls elicited by leopard and lion faeces respectively and

pooled them as calls elicited by predator faeces. Then, we tested the classification probabilities of calls produced in response to predator faeces (N = 18), African rock pythons (N = 14) and rival mongooses (N = 16). The prior probabilities for calls entered into the DFA elicited in the three contexts were: predator faeces: 0.375; African rock pythons: 0.292; rival mongooses: 0.333. The first discriminant function explained 98.3 % of the total variance. The DFA yielded an overall cross-validated correct assignment of 52.1 % (Wilk's Lambda = 0.246, $\chi^{2} =$ 60.31, df = 10, $P < 0.0001$; Figure 2) compared to 33.33% expected by chance (binomial tests: predator faeces: N = 18, P = 0.001; African rock pythons: N = 14, P = 0.424, rival mongooses: N = 16, P = 0.077). The acoustic structure of calls emitted in response to African rock pythons and rival banded mongooses did not differ (post-hoc DFA: Wilk's Lambda = 0.924, $\chi^{2} =$ 2.03, df = 5, P = 0.845). Calls elicited by predator faeces yielded a high percentage of cross-validated correct assignment to the appropriate context whereas calls produced in response to African rock pythons and rival mongooses yielded only a low percentage of correct assignment respectively and were often misclassified to the other context in which noisier calls were produced (Table 2). There were neither sex-specific call characteristics (post-hoc DFA, sex-specificity, first function: Wilk's Lambda = 0.964, $\chi^{2} =$ 1.61, df = 5, P = 0.9; binomial test: N = 48, P = 0.88) nor group-specific call characteristics (post-hoc DFA, group-specificity, first function: Wilk's Lambda = 0.483, $\chi^{2} =$ 30.1, df = 25, P = 0.22; binomial test: N = 48, P = 0.32). Furthermore, in 22 of 27 presentations of predator faeces at least one of the individuals arriving in the last quarter of all group members was calling. In all encounters with pythons and in all inter-group interactions group members continued to call after gathering together.

a)



b)



c)

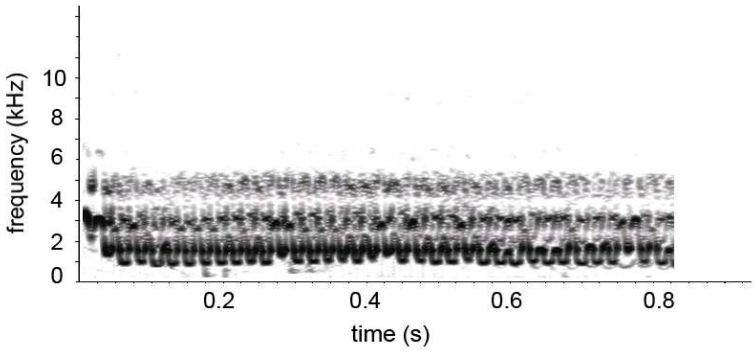


Figure 1. Spectrograms of calls produced in the context of recruitment: a) when encountering predator faeces (here lion faeces); b) at the beginning of an inter-group encounter with rival banded mongooses; and c) at the beginning of an inter-group encounter with rival banded mongooses showing intermediate acoustic structure.

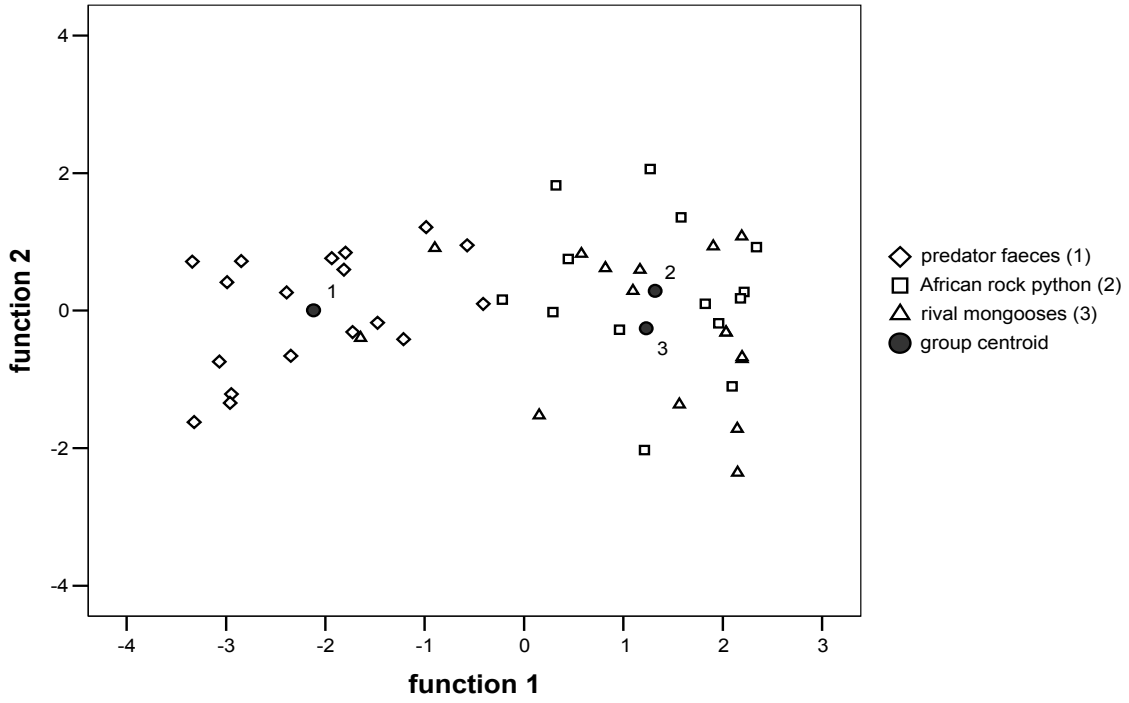


Figure 2. Discriminant function scores and group centroids of calls elicited by predator faeces (1), African rock python (2) and rival mongooses (3).

Table 2. Cross-validated percentages of assignment of analysed calls to the three given contexts: 1) Predator faeces; 2) African rock python; and 3) rival banded mongooses. Note the high percentages of incorrect assignment between contexts two and three.

		predicted group membership			
context		1	2	3	total
% cross-	1	88.9	5.6	5.6	100
validated	2	0	35.7	64.3	100
assignment	3	12.5	62.5	25.0	100

Responses to playbacks

Subjects responded to playbacks of calls elicited during the encounter of all three different stimulus types. Typically, subjects responded by looking towards the speaker, and then approaching it as a close, cohesive group. The time to approach the speaker for the first individual of the group did not vary between calls elicited by the two different secondary predator cues (leopard: 51.72 s (untransformed mean), $N = 11$); lion: 54.91 s, $N = 12$.; $F_{1,17} = 0.13$, $P = 0.72$). Therefore, we pooled the responses to calls elicited by leopard and lion faeces by randomly selecting six playbacks each. We conducted the randomization five times, and used the one with the median mean time to approach the speaker. The time to approach the speaker for the first individual of the group varied significantly between playbacks of calls elicited by predator faeces (52.83 s (untransformed mean), $N = 12$), African rock pythons (38.8 s, $N = 10$) and rival mongooses (36.6 s, $N = 10$; $F_{1,26} = 8.358$, $P = 0.008$; Figure 3). The percentage of individuals approaching the speaker varied between calls elicited by the different stimulus types (predator faeces: 53% (untransformed mean), $N = 12$; African rock pythons: 71 %, $N = 10$; rival mongooses: 76.3 %, $N = 10$; $F_{1,26} = 4.768$, $P = 0.038$; Figure 4). None of the individuals approached the speaker in any of the six control playbacks using calls of the yellow-fronted tinkerbird as stimuli.

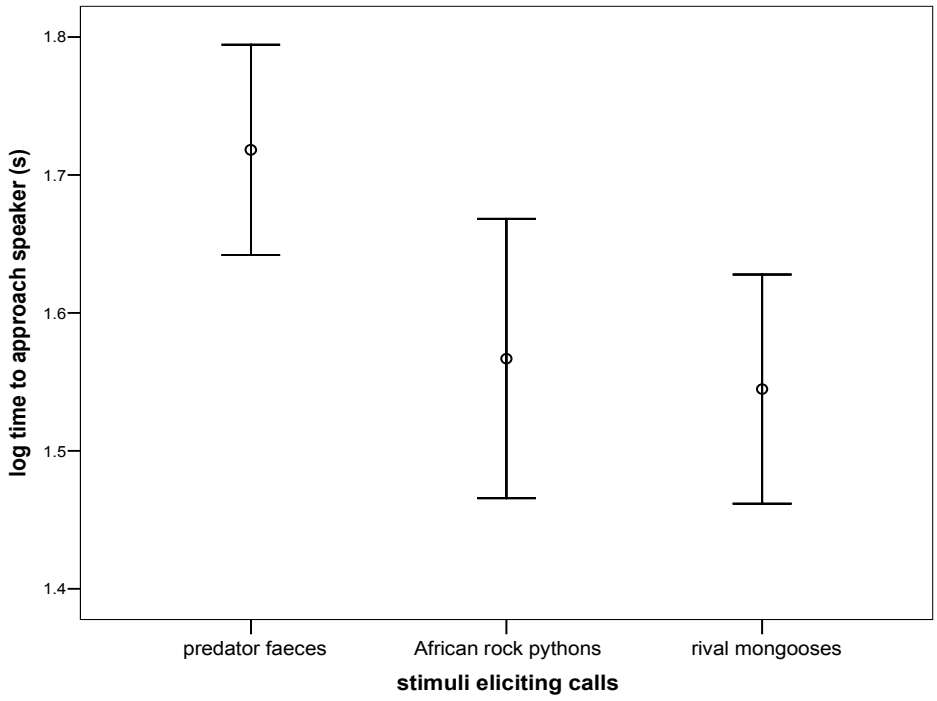


Figure 3. The time taken by the first individual to approach the speaker during playback of calls elicited when exposed to three different stimuli. Means ± SD are shown.

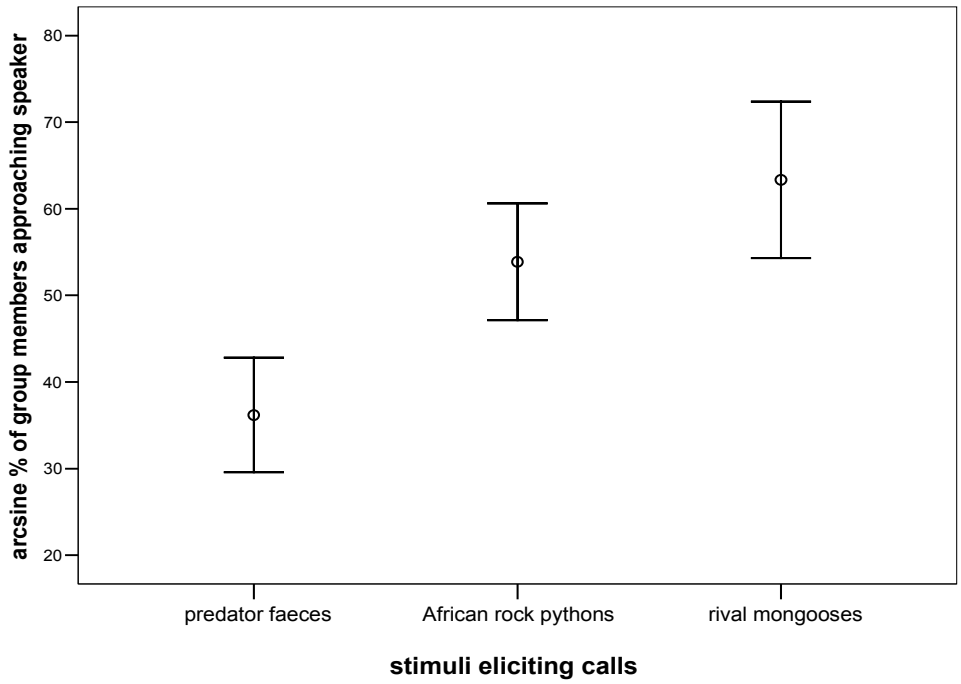


Figure 4. The arcsine-transformed percentage of individuals approaching the speaker during playbacks of calls elicited when exposed to three different stimuli. Means ± SE are shown.

DISCUSSION

In banded mongooses, recruitment calls did not convey stimulus specific information, but appeared to vary with the degree of risk faced by the caller. The acoustic structure of the calls graded from tonal variants in less risky encounters of secondary predator cues, to calls with a harsher, noisier acoustic structure produced during high-risk confrontations with snakes or rival conspecifics. The possibly higher threat level represented by leopards compared to lions was reflected neither in the acoustic structure of calls elicited in response to their faeces, nor in the response time to playbacks of these calls. The acoustic structure of calls emitted in response to African rock pythons and rival banded mongooses did not differ. A higher proportion of tested subjects approached the speaker playing calls elicited by snakes and rival mongooses and they also did this faster in comparison to playbacks of calls emitted in response to predator faeces.

The acoustic structure of the recruitment calls emitted during encounters of the three different stimuli varied greatly between secondary predator cues and snakes and rival groups. Although only very few calls of intermediate acoustic structure were elicited by all the different stimulus categories, the acoustic structure of calls elicited by predator faeces graded towards the acoustic structure elicited by the other two contexts (and vice versa), indicating a risk-based system. However, while calls elicited by snakes and rival groups greatly overlapped, there was little overlap between these calls and those elicited by predator faeces (only two calls elicited by foreign mongooses were similar in acoustic structure to those elicited by predator faeces). The lack of differences in call structure and response time suggests that banded mongooses cannot discriminate between lion and leopard faeces and respond to them acoustically in the same way. It may also be that they actually can discriminate between them, but that the level of arousal caused by lion and leopard faeces is similarly low in comparison to that elicited by snakes and rival groups. These findings may suggest that banded mongooses distinguish between discrete threat categories, specifically secondary cues and live animals. However, playbacks showed that the same response type always occurs (with differences in the speed of the response and the number of group members responding, according to the level of urgency), which suggests a graded rather than a discrete call system in the context of recruitment. Since the perceived risk for the caller might decrease with time, calls occurring later in the bout could reflect decreased urgency. This could be a confounding factor in our study as calls emitted in response to predator faeces were recorded from the very beginning of the calling bout during presentations, while calls elicited by African rock pythons and rival conspecifics were recorded with a delay of 5-15 s on occurrence. However, this potential methodological restriction is not likely to affect the validity of our results since calls produced in response to African rock pythons and rival mongooses indicate higher urgency, even though recording started with a short delay in time in these two contexts.

In addition to variation in the acoustic structure of calls, variation in call rate may also influence the receiver's responses (Blumstein & Armitage 1997; Warkentin et al. 2001). As several banded mongooses often called almost at the same time, we cannot provide a detailed analysis of the number of calls produced in the different contexts per individual. We can generally say that when encountering predator faeces, each calling individual emitted only few calls (range 1-3; R. Furrer, personal observation) and call duration by the whole group lasted from less than 1 min to up to 5 min, whereas when encountering African rock pythons

or rival banded mongooses individuals typically emitted many calls (up to 20 or even more calls depending on the severity of the encounter; R. Furrer, personal observation) and group calling could last for 15 min or more.

The acoustic variation of banded mongoose recruitment calls was not stimulus specific and therefore the calls are not functionally referential. This suggests that, in the banded mongoose, information on risk is more important than specific information regarding the external stimulus type, as the general response in the different contexts did not differ, and only the urgency level appeared relevant. The acoustic structure of recruitment calls may express the caller's emotional state at the moment of calling, with noisier call variants produced during high arousal situations (Morton 1977; Marler et al. 1992). Receivers seemed to extract specific information on the level of urgency from the acoustic structure of calls, and adjusted their speed of response accordingly. A previous study on banded mongooses indicated that receivers do not extract information on urgency levels from heterospecific alarm calls of plover species (Müller & Manser 2008). However, this may be explained by perception differences of urgency levels between mongooses and plovers or indeed by the costs of wrong responses to heterospecific alarms (Müller & Manser 2008). Although banded mongoose alarm calls given to aerial and terrestrial predators (causing receivers to become vigilant or to escape to shelter) are acoustically distinct from the recruitment calls (R. Furrer, personal observation), it is currently unknown whether they are functionally referential and refer to specific predator types. It may therefore be that alarm calls in this species are, in general, based on risk or urgency level rather than denoting an external stimulus, in a functionally referential way. It would be interesting to see whether species with confirmed predator-specific aerial and terrestrial calls, such as meerkats, have also evolved stimulus-specific recruitment calls.

Receivers responded to all non-control playback stimuli by approaching the speaker, confirming that these calls function to recruit other group members. However, since later arriving mongooses continued to call while inspecting the predator faeces and group members called for prolonged periods while mobbing a snake or facing a rival banded mongoose group, additional adaptive functions should be considered (see also Welbergen & Davies 2008). In banded mongooses it remains to be tested whether, besides physical harassment during the mobbing (Curio et al. 1978; Owings & Owings 1979; Dugatkin & Godin 1992; Graw & Manser 2007), continued calling itself could deter encountered predators and rivals. When

sighting rival mongooses, individuals started calling, which recruited other group members. The bunched group continued calling, similar to territorial vocal rallying in birds (Radford 2003; Radford & Du Plessis 2004). However, in banded mongooses calling can go beyond a form of group display, continuing during one-to-one fights and chases (Cant et al. 2002). Therefore, it may not only deter bunched rival mongooses but also discourage opponents during agonistic encounters on the individual level. Furthermore, the continued calling when encountering secondary predator cues and snakes suggests these calls may also play a role in group decision making to coordinate the response of group members. Whether these calls function imperatively (as an 'order' to approach given by the caller; Evans 1997) or are just expressions of the caller's arousal, still has to be tested. For example, this could be done in the context where a solitary mongoose encounters a secondary predator cue or predator, while separated from its group members and therefore unable to recruit them. One would predict that if calls functioned imperatively the solitary individual would not call, whereas if calls were just an expression of the caller's arousal solitary mongooses would still be likely to call.

In conclusion, the acoustic structure of recruitment calls was not stimulus-specific, but appeared to vary according to the risk of the situation. This is equivalent to mobbing calls described for birds, where calls towards different stimuli vary acoustically, in a graded manner according to size or distance of the predator (Templeton et al. 2005; Welbergen & Davies 2008). Despite different stimulus types eliciting the calls and different purposes for recruitment, a graded call system in banded mongooses seems sufficient for receivers to respond appropriately. Playbacks showed that these calls function to recruit other group members. However, since calling continues even after most or all group members are gathered, calls may also function to deter or chase off predators or rival conspecifics, or play a role in group decision making to coordinate the response of all individuals.

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GENERAL DISCUSSION

General Discussion

In the preceding four data chapters, I investigated different aspects on leadership and group decisions in the banded mongoose, a group living species with egalitarian social structure. In particular, I tried to identify factors influencing leadership in group departure and factors influencing group decisions under time constraints, as well as an acoustic mechanism in the context of recruiting other group members to the location of the caller(s). In this concluding chapter, I first discuss the importance of consensus decisions in daily lives of banded mongooses. I then review the factors influencing leadership and group decisions as well as the underlying mechanisms in the banded mongoose and put them into a broader context. Finally, I provide the conclusions and give some suggestions for further research on leadership and group decisions in banded mongooses and also more general.

The importance of consensus decision-making in banded mongooses

In consensus decisions group members choose between two or more mutually exclusive actions with the specific aim of reaching a consensus. As conflicts of interest between group members might be involved in such decisions, individuals may incur 'consensus costs' by forgoing their own optimal action (Conradt & Roper 2005). Studies suggest that whether groups make consensus or combined decisions depends on the individual's ratio between grouping benefits and consensus costs (Biro et al. 2006; Kerth et al. 2006; King et al. 2008). Thus, combined decisions, where some group members form subgroups temporarily without leaving the society permanently, can be an optimal group decision (Conradt & Roper 2005, Kerth et al. 2006). Where a consensus cannot be reached due to inter-individual conflicts or time constraints, splitting up in subgroups can be an optimal group decision (Franks et al. 2003; Kerth et al. 2006; King et al. 2008; Conradt et al. 2009). In banded mongooses, however, apart from babysitters that remain at the den with the recently born offspring (Cant 2003), social groups hardly ever split up and consensus decisions are made frequently throughout the day. This indicates that the grouping benefits generally outweigh the consensus costs. With this in mind, the question arises which factors lead to these high benefits of consistently remaining in the group in banded mongooses.

As small-bodied, ground-dwelling, diurnal mammals banded mongooses are prone to be preyed on by different predator types. In search of their invertebrate and small vertebrate prey, banded mongooses' heads commonly point towards the ground and their eyes are sometimes underneath the surface of the soil when digging for prey, preventing them from seeing far, which renders them vulnerable to predation. Thus, staying together with the other group members might substantially enhance predator detection and enables to profit from alarm calling. Additionally, close group cohesion provides individual protection when facing predators. Group members bunch together to attack snakes or small mammalian predators (Rood 1975) and a group of banded mongooses was even observed to rescue an individual from an eagle (Rood 1983). Thus, it is likely that consensus decisions during foraging improve the individuals' survival chances. This assumption is supported by findings from the closely related meerkats (*Suricata suricatta*), where single individuals and small groups suffer much higher predation than larger groups (Clutton-Brock et al. 1999). Furthermore, contests with rival groups can have fatal consequences in banded mongooses (Rood 1975; Cant et al. 2002; Gilchrist & Otali 2002). As inter-group encounters are normally decided by group size with the larger group defeating the smaller one (Cant et al. 2002), it is essential that group members make consensus decisions and stay together in such contests.

Apart from predation and inter-group contest, the social organization of banded mongooses is likely to influence the strong group cohesion mediated via consensus decisions. Groups of banded mongooses breed up to five times per year and, during each breeding attempt, multiple females come into oestrus in synchrony and mate with multiple males within the group (Cant 2000). The egalitarian social system of banded mongooses stands in strong contrast to the despotic system of meerkats where normally only the dominant female breeds and the dominant male fathers the offspring (Griffin et al. 2003). While in meerkats it may pay off for subordinate males to leave the group temporarily and become rovers in search of extra-group copulations (Young et al. 2007), in banded mongooses such prospecting forays by males only very rarely occur. For them, staying in their own group, monitoring the females' reproductive state and trying to mate with one or several females during their synchronized oestrus appears to be a more successful strategy. After gestation, 1 to 10 females give birth synchronously to a communal litter. Up to 19 pups have been observed after birth when individuals first moved pups to another den (Roman Furrer, personal observation). Until pups forage independently, group members assist in rearing the pups by provisioning them with food items (Gilchrist 2004; Hodge 2005). To successfully provide food for a large number of pups it might be

crucial to maintain group cohesion via consensus decisions. Individuals may benefit from grouping by gaining a greater overall vigilance than solitary animals, allowing them to spend more time on non-vigilant behaviours such as foraging and provisioning food for pups (Bertram 1980). Overall, in banded mongooses, the high grouping benefits seem to be influenced by the high predation pressure, the stiff competition between different social groups and the egalitarian social system. To maintain their high group cohesion consensus decisions are not only likely to be of particular importance but also appear to have positive fitness consequences for the individual.

Initiation of group departure in banded mongooses: influencing factors and underlying mechanisms

Studies dealing with consensus decisions about activity timing and travel destinations have shown that these decisions are often initiated by a single leader (Kummer 1968; Dunbar 1983; Lamprecht 1992; Beauchamp 2000; Leca et al. 2003). In such coordinated group movements, certain individuals may act consistently as initiators or variable individuals might emerge spontaneously as leaders (Conradt & Roper 2005). The factors influencing such leadership roles have been widely discussed (Erhart and Overdorff 1999; Reebs 2000; Rands et. al 2003; Ward et al. 2004; Leblond & Reebs 2006; Fischoff et al. 2007; Jacobs et al. 2008; Sueur and Petit 2008; Harcourt et al. 2009). In banded mongooses, leadership in group departure is highly variable with most adult individuals being observed to initiate group movement (chapter 1). Neither sex nor age influenced leadership roles overall. However, pregnant females tended to initiate and lactating females initiated group departure more often than expected. These findings suggest that the energetic state of the individual might be more important than the individual's identity, as shown in other species (see Fischhoff et al. 2007). The initiator's weight in relation to its weight of the previous day was lower than the weight balance of a control period (chapter 2). However, the weight difference was not significant as there was high variability in the data suggesting that factors, such as high energetic demands during periods of pregnancy/lactation, asymmetries in foraging ability and the foraging time available might be equally important as short-term foraging success. Thus, it seems that in social groups with individuals of different age, sex and different abilities as well as different time available for foraging, the resulting changes in behaviour may be complex (Rands et al.

2008) and no single factor may be the key determinant of leadership roles. Interestingly, the results of deprivation of food/feeding experiments contradicted these findings (chapter 2). In the experimental design, where exactly half of the subjects were deprived of food and the others fed, low energetic reserves became important. In line with predictions from game-theoretical modelling (Rands et al. 2003), the food-deprived individuals tended to become pacemakers in initiating group departure. The combined results of the weight data and of the manipulation of foraging success suggest that, in an experimental setup, nutritional constraints can be the key determinant of leadership in banded mongooses. Similarly, studies in other species have shown that a single factor like energetic reserves, knowledge about resources, personality or dominance can have a high influence on leadership in group movement (Rands et al. 2003; Seeley 2003; Ward et al. 2004; Sueur and Petit 2008). However, in species that live in social groups with asymmetries between individuals and in particular in cooperative breeders such as banded mongooses, where the investment in cooperative activities commonly differs among helpers (Cockburn 1998), the determining factors underlying leadership in movement decisions might often be diverse.

As group departure in banded mongooses was clearly initiated by a leader, who often produced moving calls at the onset of movement, indicates that this leader makes a despotic group decision on behalf of all other group members. However, the success of initiation attempts was influenced by the production of moving calls of other group members (chapter 1). Individuals showing a higher proportion of immediate followers producing moving calls during their initiation attempts had a higher success ratio. Hence, it seems that often other individuals contribute to the decision to depart by producing moving calls right at the onset of movement. To successfully lead the group away from the den, acoustic votes of followers were important and thus the decision-making often seemed to be partially shared. Whether the process of decision-making relies on a quorum (minimum number of group members that need to favor a particular action for the whole group to adopt this action, Conradt & Roper 2005) cannot be answered yet. Before group departure, banded mongooses often stayed very closely together and then departed with individuals moving in a file, either single or up to three animals abreast (Rood 1975). Therefore, it was not possible to count the exact number of callers. In my study I only focused on whether the leader was calling and whether at least another individual produced calls. To shed light on a possibly involved quorum threshold one would need to know the exact number and proportion of group members calling during group departure. To determine which individuals called during a particular initiation attempt, one

could try to put audio-collars on the mongooses' necks. Whether despotic or partially shared, the initiation of group departure in banded mongooses appears to be facilitated by global communication within the social group with leaders and followers often producing specific moving calls. Whether moving calls function to initiate group movement of a stationary group and/or help to steer the direction of travel at and just after the onset of movement (see Boinski 1991; Boinski et al. 1994; Boinski and Campbell 1995; Radford 2004; Trillmich et al. 2004) still needs to be tested with playback experiments.

Group decision-making in a potentially dangerous situation: influencing factors and underlying mechanisms

Group decisions in potentially dangerous situations are predicted to differ in their underlying mechanisms to the routinely decisions about when to leave the den or where to go foraging (Conradt & Roper 2005). With playbacks of screeching calls I simulated a group of intruding banded mongooses and analysed the resident group's decisions in response to this stimulus (chapter 3). After the resident group had gathered, subjects responded strongly and moved as a unit either towards the speakers or in the opposite direction further away from them. In our playbacks, the largest group always moved towards the speakers whereas the smallest group always retreated, independent of the experiment location. These findings suggest that in situations of impending inter-group encounters, where it is often difficult to assess the opponent's strength in numbers, experience of previous encounters plays an important role in the decision-making process. Previous results have shown that in banded mongooses the larger group normally wins such inter-group contests (Cant et al. 2002). Thus, it is likely that in our simulated impending contests the largest group's decisions to always advance were based on experience of previous encounters. Furthermore, analysis showed the four medium-sized groups responded context-specifically with retreating in the overlap zone and advancing in the core zone suggesting that range defense is higher in the centre of the territory. These results are in line with predictions of the evolutionary game theory suggesting that the expected benefits may vary with the location relative to the opponents' territorial boundaries (Maynard Smith 1982). Results derived with automated radio telemetry during inter-group contests in capuchin monkeys (*Cebus capucinus*) showed that small resident groups can defeat larger groups near the centre of their home range (Crofoot et al. 2008). Hence, our findings indicate that group size and encounter location are not only important factors determining the

outcome of inter-group encounters (Crofoot et al. 2008) but also influence the group decisions at the beginning of an impending encounter.

In the simulated impending contests, the resident group had to decide fast whether to retreat or to attack as the intruders, who had already perceived them (otherwise the intruders would not have started producing screeching calls), might have attacked very soon. In such situations which require fast responses under time constraints, despotic decisions made by experienced or best-informed group members should be favored (Franks et al. 2003; Passino & Seeley 2006). Indeed, in some of the playbacks, the coordinated group movement in response to calls of intruders appeared to be initiated by a single individual. However, we could often not determine the identity of this leader. The leader moved, often emitting moving calls, either towards or away from the speakers. The other group members followed immediately and the group moved as a single unit. However, in other experiments all subjects almost simultaneously started to move in the same direction with no obvious individual initiating group movement. Thus, while sometimes a leader with global control seemed to initiate the group response, in other experiments, where individuals responded synchronously, global control by particular individuals appeared not to be involved in the decision-making. In fast coordinated responses, subjects do not seem to be able to communicate with all other group members. Thus, in such situations, consensus decisions are probably restricted to self-organizing rules, where individuals depend on local communication with their spatial neighbours (Seeley & Visscher 2003; Couzin et al. 2005). Such coordinated behaviour without the need of global control also occurs in flocks of birds (Conradt & Roper 2000), shoals of fish (Krause et al. 2000), herds of mammals (Gueron et al. 1996; Prins 1996) and social insects (Seeley & Buhrman 1999; Franks et al. 2003). Whether these immediate decisions were made despotically, partly shared or even democratically still has to be investigated. With cameras installed above the gathered subjects one might be able to determine the leader's identity and to analyse the mechanisms underlying the decision-making in simulated inter-group encounters more into depth.

An acoustic mechanism to recruit other group members and its implications for group decision-making

Studies have shown that different species of birds and mammals use specific calls that recruit conspecifics to the location of the caller (Collias & Joos 1953; Stokes 1971; Elgar 1986; Marler et al. 1986a; Marler et al. 1986b; Marzluff & Heinrich 1991; Manser 2001; Manser et al. 2001; Radford & Ridley 2006). Banded mongoose's recruitment calls vary in their acoustic structure according to the context and receivers extract meaningful information from these differences (chapter 4). Calls recorded while individuals encountered secondary predator cues differed from the variants elicited by snakes and rival groups, but not between the latter two. Playbacks of calls elicited by the different stimuli caused individuals to approach the speaker in the same way. However, calls elicited specifically by snakes and rival mongooses resulted in a higher proportion of receivers responding and a faster receiver response, in comparison to calls elicited by faeces. These findings suggest a graded rather than a discrete call system in the context of recruitment. In contrast, in Siberian jays (*Perisoreus infaustus*), mobbing calls encode simultaneously information about both predator category and the risk posed by a predator (Griesser 2009). Jays discriminate between predator categories and utter two hawk-specific and three owl-specific call types. For them the ability to communicate the predator category during mobbing might be adaptive because it may allow other mobbers to adjust the risk they take. In banded mongooses, however, as indicated by the name, recruitment calls occur not only during mobbing but function to recruit other group members to the caller's location. After having arrived at the location of the caller(s), the gathered group members see the stimulus and then decide whether to approach and mob/fight or to retreat might be appropriate. In banded mongooses the individuals' decisions on which activity to perform appear to rely on an assessment of the gathered group members prior to mobbing. Thus, in banded mongooses the selection pressure to evolve calls that convey information about predator category may not have been very strong and recruitment calls that vary according to risk might convey all important information needed.

In banded mongooses, recruitment calls appear to be an efficient acoustic mechanism allowing group members to gather quickly at the location of the caller(s), which ensures that all group members gain information about the encountered stimulus. This communal information gathering seems to be crucial as mathematical logic implies that, even if the most

experienced individual found the stimulus first, its potential error in despotic decision-making would often be larger than the combined errors of several inexperienced group members (Conradt & Roper 2003: List 2004). When banded mongooses for example find a secondary predator cue, the gathered information could either reveal that the cue is very fresh and thus it is likely that the predator is close-by or inspection could indicate that the predator is unlikely to be in the vicinity as the cue is already relatively old. The costs of wrong decisions in this example might be high as unnecessary avoidance of an area where the predator is unlikely to be encountered anymore might lower the individual's foraging success as food availability in this unexploited area may be high. On the other hand misinterpreting fresh predator cues could have fatal consequences for certain group members. Thus, decision-making based on communal information gathering about the encountered stimulus appears to have direct fitness consequences for the individual as it has been shown that the error in the information available to the whole group is smaller than the error of a solitary decision-maker (Conradt & Roper 2000; Mallon et al. 2001; Conradt and Roper 2003; Franks et al. 2003; Simons 2004).

Conclusions

My study dealt with leadership and group decisions in banded mongooses, a social carnivore with low reproductive skew among females. Because of their egalitarian social system, which stands in strong contrast to the despotic social systems of a single breeding pair in closely related species (meerkats, dwarf mongooses), banded mongooses offered exciting possibilities to compare and contrast factors that might influence group decisions in social mongooses. Due to the availability of life-history data and good habituation levels of individuals I found that a variable state like the females' reproductive state can influence leadership in group decisions more strongly than the individual's identity. This result stands in contrast to results from other studies showing that fixed factors like age, sex and personality traits or variable but long-lasting factors like dominance rank were determining leadership roles in group decisions. A study in seasonally breeding meerkats underlines the importance of analyzing variable factors such as the female's reproductive state as it showed that the dominant female initiates group departure more often while lactating compared to non-reproductive periods (Turbé 2006). The combined results derived from banded mongooses and meerkats underline that

high energetic requirements, for example during breeding periods, may override the influence of dominance on leadership roles.

The possibility to weigh individuals in the field and conduct short-term deprivation of food/feeding experiments revealed that nutritional constraints caused by a bad foraging success appear not to be the sole key determinant of leadership roles. This result suggests that in cooperative breeders, and particularly in species with egalitarian social structure, where many asymmetries between individuals may frequently occur, various factors appear to influence leadership roles overall. These findings stand in contrast to studies of leadership in pairs of animals, which often provide clear-cut results by underlining the importance of a single factor in determining leadership roles (Rands et al. 2003; Harcourt et al. 2009). Thus, I expect that in-depth analyses of several factors will show that also in other group-living species leadership in movement decisions depends on several factors and their interactions. I furthermore predict that in other social animals, the current state of an individual may often have a higher influence on leadership in group decisions than the individual's identity.

Previous research has stressed the impact of the encounter location and the group size on the outcome of territorial contests between groups of animals (Crofoot et al. 2008). My results reveal that in simulated inter-group encounters, where I was able to analyse the resident group's behaviour at the beginning of an impending contest, encounter location, group size and potentially experience gained during previous contests, influence the group's decisions prior to the actual contest. It would be interesting to see whether the same factors have an impact on group decision in impending dangerous situations in other species and particularly in species with other social organizations.

Banded mongooses emit specific calls when encountering secondary predator cues, snakes or rival mongooses. My analyses reveal that these calls function to recruit other group members to the location of the caller(s) and show that receivers adjust the speed of their response according to the risk faced by the caller. The decision whether to advance/mob/attack or to retreat is made by the assembled group members after they gathered. Thus, in banded mongooses, a graded call system, where the calls' structures vary according to the risk, provides all information needed to respond appropriately. It will be interesting to see whether further species apart from Siberian jays have evolved stimulus-specific calls and why such recruitment calls may have evolved.

Future directions

Due to the relatively large group sizes of the study groups, some mechanisms involved in the initiation of group departure and in the response towards screeching calls of intruders could not be studied in a detailed manner. Some technical additives such as audio-collars to analyse possible quorum thresholds in moving calls produced by followers or cameras that would allow more sophisticated filming of the resident group's responses towards screeching calls of intruders could lead to further insights into subtle mechanisms underlying group decisions. For example one could analyse whether possible quorum thresholds involved in group departure might vary according to group size and compare and contrast them with findings of closely related species (e.g. meerkats) or even compare them with potential quorum thresholds observed in group decisions of human crowds. Furthermore, if one could confirm that self-organizing rules would be involved in fast consensus decisions in simulated dangerous situations, one could potentially try to analyse what factors influence the shift from decisions initiated under global control to decisions where self-organizing rules underlie the decision-making. Thus, banded mongooses still offer a wide variety of opportunities to study leadership and group decisions and in particular mechanisms underlying them in future.

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